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# Contextualizing the clock(s) : integrating cues for the perception of time and timing an action

Ljubica Jovanovic

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# THÈSE DE DOCTORAT

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PSL Research University

Préparée à École Normale Supérieure

Contextualizing the clock(s): Integrating cues for the perception of time  
and timing an action

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# Abstract

Humans can discriminate temporal intervals in a vast range of durations. They can extract temporal patterns, organize, and execute complex motor behaviors

To understand human time perception, we need to be able to explain why and how different aspects of the context affect temporal judgements. In this thesis I investigated how different aspects of human time perception are affected by context.

The prominent models of duration perception assume that at the onset of the duration to be timed there is a mandatory resetting of the time mechanism. In Part 1 of the thesis, I investigated how cues for resetting the clock affected perceived elapsed time between two moments. The two hallmarks of time perception, the scalar variability of time and the regression to the mean, were found both when the interval to be timed was cued beforehand, or revealed retrospectively. Nevertheless, the effects were different for the two conditions: the temporal context affected the estimates more in the implicit onset condition, and the estimates were more biased towards the mean of the presented durations, and sensitivity of duration discrimination sensitivity was lower in the condition with no explicit onset of the duration to be timed.

The manner in which events from a different or the same modality affect when an event is perceived is addressed in Part 2. The findings from the three projects presented suggest that the perceived time of events can easily be biased by the temporal and spatial context. Findings in these studies support the hypothesis that the perceived time of (visual) events does not always correspond to the perceptual latencies measured in the reaction time tasks, and that the saliency is an important cue for the perceived time.

Finally, in Part 3, I investigated how different sources of uncertainty affect the timing and self-evaluation of an action. The findings suggest that timing an action and evaluating its outcome may at least in part, rely on different computations.



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# Introduction

Humans can discriminate temporal intervals in a vast range of durations. They can extract temporal patterns, organize, and execute complex motor behaviors. Furthermore, the temporal structure of the environment can be used to predict when an event is going to occur, so as one can act accordingly. However, relevant events in our environment do not appear isolated from the complex, multisensory stream of information we are constantly exposed to. On the contrary: sounds, images, and vibrations from events in our environment continuously reach our sensory organs, overlapping in space and time. Time perception is malleable, and numerous time illusions suggest that the perceived time of events is affected by context (Eagleman, 2008; Matthews & Meck, 2014). Furthermore, our internal states, such as attention (Brown, 1985), emotions (Droit-Volet & Meck, 2007), intention to act (Binetti et al., 2015; Wenke & Haggard, 2009), and even body temperature (Aschoff, 1998; Wear-den & Penton-Voak, 1995), can affect the perception of time.

To understand human time perception, we need to be able to explain why and how different aspects of the context affect temporal judgements (Matthews & Meck, 2014). The *context* here refers to different features of the environment, such as events that completely or partially overlap in time and space, or cues that may bias or optimize performance (Albright & Stoner, 2002).

In this thesis I investigated how different aspects of human time perception are affected by context. First, the project presented in Part 1 investigates how cues for *resetting* the clock affect perceived elapsed time between two moments. The manner in which events from a different or the same modality affect when an event is perceived is addressed in Part 2. Finally, in Part 3, I investigated how different sources of uncertainty affect the timing and self-evaluation of an action. Before describing the research and discussing the findings, I will review previous work relevant for the questions addressed in this thesis.

In the Introduction I will first present a spectrum of views on the main dimensions of human time perception. Then, I will review the literature regarding how the context of an event affects perceived time and duration. Finally, I will present different models developed to explain the human perception of duration and of ordering events in time.



# Chapter 1

## Literature review

The perception of time is a broad concept. It encompasses rhythm and rate perception, simultaneity and temporal order discrimination, duration perception and reproduction (Pöppel, 1997; Van Wassenhove, 2009). For the scientific study of time perception it is pertinent to define a meaningful taxonomy of time (Meck & Ivry, 2016; Paton & Buonomano, 2018). This is an ongoing endeavour in the time research community (Meck & Ivry, 2016), and I will not attempt to solve this issue here. I will, however, present different views on what the principal dimensions of human time perception are, in order to frame the scope of this thesis.

Fraisse (1984) proposed that the concept of time consists of two concepts: succession and duration. To perceive succession, we need to perceive two distinct events in sequence. The perception of duration is the perceived interval between those two events. The two notions are hierarchical, since perceived succession precedes the percept of duration between two successive events. We can further distinguish between the perceived relative and apparent time of events (Arnold, 2010; Van De Grind, 2002). Relative time refers to the apparent time of one event in relation to another. Apparent time is the moment when an event is perceived to occur (Arnold, 2010; Libet, Gleason, Wright, & Pearl, 1983; Van De Grind, 2002). I will discuss apparent time in greater detail in Part 2 of the thesis.

We can also distinguish between implicit and explicit timing, depending on whether temporal information is used for acting on the environment, or to reflect upon conscious experience (Michon, 1990). For instance, in classical conditioning, temporal information is processed, but not explicitly evaluated, as it is in explicit duration judgements (Ivry & Spencer, 2004). Similarly, depending on the degree to which temporal structure in the environment is analysed, as opposed to imposed on the environment, we can distinguish between sensory and motor timing (Paton & Buonomano, 2018).

In summary, the myriad of behaviors that human time perception comprises



can be systematized in different ways. These distinctions should reflect complementary, but distinct computations, that rely on (at least partly) different mechanisms and representations (Marr, 1982). In this thesis I investigated perceived duration and perceived apparent time of events (Part 1 and 2). Work presented in Part 3 addresses anticipatory motor timing.

In order to carry out scientific investigations of perception of time, it is important to apply appropriate behavioral measures. In addition, it is pertinent to understand which aspects of behavior different methods assess, as well as underlying assumptions, and limitations. I will outline the most commonly used measures used in time perception research in the next session.

## 1.1 Behavioral techniques for investigating time perception

In this section I will address the most commonly used behavioral methods for investigating perceived time: duration reproduction, temporal bisection and generalization, temporal order, and simultaneity judgements. I will not address *comparison methods* (e.g. Wearden, 2016), since they are classical psychophysical methods of constant or single stimuli with variable interval durations as stimuli.

### 1.1.1 Temporal Reproduction and Production tasks

If we are interested in the perceived duration of certain events or elapsed time between two temporal markers, the most straightforward task is to ask participants to *reproduce the duration* of the stimulus. In the temporal reproduction task, observers reproduce the duration of the stimulus, usually with a manual response (e. g. hold down, release, double press some key). The type of motor response that is required can affect the accuracy and precision of the measurement (Mioni, Stablum, McClintock, & Grondin, 2014). In particular, when participants press the key at the onset and offset of the interval, temporal estimates are less biased than when participants hold down a single key. In contrast, the greatest precision is obtained with continuous key presses (Mioni et al., 2014). The reproduction task is often used in retrospective time perception studies, in which participants do not know beforehand that they will be asked to report duration (Wearden, 2016).

In the interval *production* task, participants are asked to produce the target duration, with no presentation of a stimulus. Biases in the interval production task are assumed to give an insight into the intrinsic biases of the internal timing mechanism.

Both reproduction and production tasks give measures of bias and variability of temporal perception and estimation. However, variability can be corrupted by motor noise (Mamassian, 2008), and biased by differences in the time needed to prepare and execute movement (Droit-Volet, 2010). Moreover, interval production and reproduction tasks cannot be used to investigate the perception of time of very short durations, due to the temporal limits of motor execution.

### 1.1.2 Temporal Bisection and Generalization

A widely used task, particularly in animal research, is the *temporal bisection* task (Penney & Cheng, 2017; Wearden, 2016). In this task, participants first learn two reference durations, *short* and *long*. After a learning phase, participants are presented with intermediate durations, and their task is to estimate whether the presented duration is more similar to the short or long reference. From the frequency of categorization of intermediate durations, we obtain the *bisection point*: the duration that is categorized as short or long equally often. In addition, we can obtain an estimate of discrimination sensitivity. Since participants use an internal criterion for categorizing durations as short or long, this task is useful in experiments investigating biases due to adaptation or context. It has been found that the bisection point is close to the arithmetic mean for linearly spaced durations and near geometric mean for logarithmically spaced durations.

In the *temporal generalization* task, participants are presented with a single standard duration, and multiple test durations that are shorter or longer than the standard (Penney & Cheng, 2017; Wearden, 2016). The participants' task is to categorize test durations as shorter or longer than the standard duration. As in the bisection task, we can obtain measures of bias and discrimination sensitivity of duration.

### 1.1.3 Temporal Order Judgements and Simultaneity Judgments

Two measures commonly used to investigate the relative timing between two events are *temporal order judgements* (TOJ) and *simultaneity judgements* (SJ). In both tasks, participants are presented with two successive stimuli, with varying magnitudes of lag between them. The temporal lag between the two signals is varied and presented multiple times, usually following the method of constant stimuli or a staircase method (Yarrow, Martin, Di Costa, Solomon, & Arnold, 2016). In TOJ task, participants are asked to estimate which of two signals was presented first (or second). In the SJ task, participants report whether the two signals were simultaneous or not. In TOJ tasks, the point of subjective simultaneity is usually defined as a stimulus intensity for which there is 50% responses that one signal

is before the other. The window of integration is defined as duration between the two unisensory stimuli that corresponds to a 75% probability of correctly detecting their order. In simultaneity tasks, the point of subjective simultaneity is the mean of the frequency distribution of *simultaneous* answers, and the temporal window of integration is defined as the temporal interval between stimulus pairs for which the two stimuli are judged to be presented in synchrony with a probability greater than some threshold (for example, 50%). In the simultaneity judgement task, the proportion of simultaneous answers is calculated for each temporal lag. In order to extract meaningful performance parameters, a function such as the Gaussian distribution, is usually fitted to the data. Since the function is not derived from an observer model, this practice has been criticized (Yarrow et al., 2016) (Yarrow et al., 2016). For instance, in a simple observer model, participants evaluate (noisy) difference in latencies of the two signals against some criterion value in order to estimate whether the two signals were simultaneous or not. In that case, the difference of two cumulative Gaussians would be a more theoretically plausible model to fit the data (Yarrow, Jahn, Durant, & Arnold, 2011; Yarrow et al., 2016).

Several studies have investigated the extent to which TOJ and SJ are related (Linares & Holcombe, 2014; Love, Petrini, Cheng, & Pollick, 2013; Van Eijk, Kohlrausch, Juola, & Van De Par, 2008). For example, Love et al. (2013) investigated the correlation between SJ and TOJ within the same group of participants with five different stimulus types, varying in complexity. Subjective reports of task difficulty revealed that TOJ were estimated as more difficult. These reports are consistent with two stage models of succession perception, in which asynchrony detection and order identification are two hierarchical processes (Jaśkowski, Jaroszyk, & Hojan-Jeziarska, 1990). In general, subjective synchrony is biased towards visual stimuli leading, while for temporal order judgements auditory stimuli had to lead the visual ones in order to be perceived as simultaneous. No correlation was found for points of subjective equality nor the size of the temporal integration window. The estimated temporal window of integration was variable across tasks and stimuli (from 128 to 279 ms). Similar results were obtained in a study where perceptual latencies between auditory and visual signals were assessed by TOJ, SJ and duration discrimination judgements (Linares & Holcombe, 2014). Moreover, a neuroimaging study revealed differential brain activation for the two tasks (Miyazaki et al., 2016).

Taken together, these results seriously question the mechanisms underlying TOJ and SJ tasks. Differences possibly stem from different biases in criterion or the order of presentation (Linares & Holcombe, 2014). In addition, the two measures can reflect partially different processes (Vatakis, Navarra, Soto-Faraco, & Spence,

2007; Zampini, Shore, & Spence, 2003). Specifically, temporal order judgements could reflect temporal discrimination and instructions could facilitate segregation of signals. On the other hand, simultaneity judgement tasks could promote binding of the two signals. The reason for discrepancies between the two measures is, at least in part, the fact that the performance measures, such as the point of subjective simultaneity, or the mean of the simultaneity judgement distribution, are not differentiating sensory, decisional, and response components of the estimation (García-Pérez & Alcalá-Quintana, 2012; García-Pérez & Alcalá-Quintana, 2017). Unfortunately, since we still lack theories of succession perception and temporal order perception, as well as neural correlates of these functions, we cannot conclude what the two measures capture, and why they are different. Modified tasks based on observer models of simultaneity judgements are proposed in order to overcome some of these problems (García-Pérez & Alcalá-Quintana, 2012; García-Pérez & Alcalá-Quintana, 2017; Yarrow et al., 2016).

Temporal order judgements and simultaneity judgements are widely used in multisensory research. On the other hand, using these tasks to investigate relative timing between events in the visual modality may be problematic, as events need to be either spatially disparate or of different size or shape, which could bias judgements (Bachmann, Pöder, & Luiga, 2004a). Nevertheless, some biases induced by the spatial layout of stimuli can offer interesting insights into the processing of succession (Giersch et al., 2015). For example, when stimuli are presented to the left and right of the fixation point, participants are generally biased to respond with the key that corresponds to the location of the stimulus (Hommel, 2011). This bias was investigated in a temporal order judgement task. Interestingly, for asynchronies below discrimination thresholds, as brief as 8 ms, this bias was systematically observed (Giersch et al., 2015). Participants from the healthy population responded more frequently to the side where the second stimulus was presented, while patients with schizophrenia responded to the first stimulus.

#### **1.1.4 Reaction time as a measure of perceived time**

Reaction time is a temporal interval between stimulus presentation and motor response. It reflects two components: latency of processing time and the motor response (Jaskowski, 1996). Reaction time and temporal order judgements are assumed to reflect the processing latencies (Gibbon & Rutschmann, 1969; Jaskowski, 1996). However, reaction time can be dissociated from explicit temporal judgements (Johnston & Nishida, 2001; J. Rutschmann & Link, 1964; Stone et al., 2001; Tappe, Niepel, & Neumann, 1994). For example, Tappe et al. (1994) found slower

reaction times to high spatial frequency gratings compared to low spatial frequency gratings, but participants' temporal order judgements were unaffected by spatial frequency, suggesting that the two measures can be dissociated. Discrepancies in the two measures were explained by postulating that reaction times and temporal order judgements come from two distinct processes (Jaskowski, 1996; Sternberg, Knoll, et al., 1973). When performance on the two tasks is registered for the same stimuli and on the same trial (Cardoso-Leite, Gorea, & Mamassian, 2007), a complex relationship between the two measures is found. In particular, the two measures seem to result from related processes, even though there are discrepancies between the two measures, probably due to decisional individual strategies (Cardoso-Leite et al., 2007).

An interesting question is whether perceptual latencies reflect the perceived time of events (Arnold & Clifford, 2002a; Moutoussis & Zeki, 1997c; Nishida & Johnston, 2002). This question will be discussed in more detail in Chapter 6.

The tasks discussed in this section are used to investigate duration or relative time between events. With an exception of reaction time, they cannot directly address when an event is perceived. In addition, reaction times may not be a good measure of when events are perceived, and the relationship between this measure and other measures of perceived (relative) time is not clear.

## 1.2 Contextual effects in time perception

Effects of context on the processing of temporal information can offer important insights into representations of temporal information, and reveal underlying processing mechanisms. Moreover, these effects constrain, inform and test different models of time perception.

### 1.2.1 Perceived time of multisensory events

Understanding how unisensory signals are integrated provides important insights into the processing of temporal information. For example, we can ask at what processing stage temporal information is encoded in the brain; whether it is before or after the integration of multisensory information.

In this subsection, I will discuss the window of temporal integration for stimuli from different modalities. Then, I will present evidence of how the brain resolves conflicts in perceived succession or duration between the senses, after a single or

repeated exposure to sensory conflict. Finally, prominent models of how multisensory information is integrated will be discussed.

### 1.2.1.1 The temporal window of integration for multisensory stimuli

Temporal coincidence is an important factor for multisensory interactions to occur (McDonald, Teder-Sälejärvi, Heraldez, & Hillyard, 2001; Meredith, Nemitz, & Stein, 1987). In psychophysical experiments, the window of temporal integration for multisensory stimuli is usually assessed by means of temporal order judgements (TOJ) or simultaneity judgements (SJ). One of the first studies that investigated sensitivity for the temporal order between stimuli from different modalities (Hirsh & Sherrick, 1961), found very low thresholds of about 20 ms. Thresholds were similar across modality pairs (visual, auditory and tactile stimuli were tested). However, more recent studies did not replicate these low thresholds. When tested with simple, transient stimuli (such as beeps and flashes), temporal order was discriminable for durations between audiovisual pairs, from 25 to 50ms (Keetels & Vroomen, 2005; Vidal, 2017; Zampini, Guest, Shore, & Spence, 2005; Zampini et al., 2003). The threshold is higher for audio-tactile (80 ms) and visuo-tactile (35-65 ms) (Keetels & Vroomen, 2008; Spence, 2013; Zampini et al., 2005) stimuli than for audio-visual pairs. The temporal window has been found to be as large as 215 ms between a pure tone beep and the brief presentation of a white annulus (Stevenson, Zemtsov, & Wallace, 2012). Thresholds for detecting the order between two signals from different modalities also vary as a function of stimulus complexity. They are smallest for brief and transient stimuli (Fujisaki & Nishida, 2005) and increase with stimulus complexity. For example, for audio-visual speech perception, the temporal window can be as large as 200 ms (van Wassenhove, Grant, & Poeppel, 2007). Perceived simultaneity is usually asymmetric: and auditory stimulus needs to lag for about 30ms to be perceived simultaneous with a visual one (Alais & Carlile, 2005).

Temporal order is more easily discriminated for stimuli that are spatially disparate (Vidal, 2017; Zampini et al., 2005, 2003). Thresholds could be improved in this condition since shared spatial location affects the probability that the two events have the same source. Furthermore, spatial location could serve as an additional cue for performing the task. Nevertheless, these studies suggest that the spatial relation between stimuli is an important factor to consider when designing a multisensory timing study.

### 1.2.1.2 Temporal ventriloquism

When an auditory and a visual event, such as an actor's voice and a puppet's mouth, are presented at two different locations, the position of the sound is attracted (captured) by the position of the visual information. The effect is usually referred to as the ventriloquist effect (Slutsky & Recanzone, 2001). Ventriloquism in the temporal domain, that is attraction in time between events from different modalities drew the attention of researchers much later (Vroomen & Keetels, 2010). In one of the first studies on the temporal ventriloquist effect, participants were asked to estimate the temporal order between two visual stimuli, presented at different spatial locations (Morein-Zamir, Soto-Faraco, & Kingstone, 2003). Two auditory stimuli were presented either before the first and after the second visual stimulus, or between the two visual stimuli (*AVVA* and *VAAV* conditions, respectively). Discrimination of temporal order was more difficult in *VAAV* condition, indicating that the moment when the visual stimuli were perceived was attracted towards the timing of the auditory events. Furthermore, it was shown that it was the second sound that was responsible for the effect; the effect was found for intervals between the two signals as large as 200 ms (Morein-Zamir et al., 2003). However, since the effect in these studies is measured by changes in discrimination sensitivity of the temporal order between the two visual stimuli, they cannot directly show by how much the perceived time of a visual stimulus is attracted to the time of the auditory stimulus. More specifically, the discriminations thresholds inform us only about the difference in time of the two subsequent visual that is needed for the temporal order between them to be detected. Studies that followed these first demonstrations of temporal ventriloquism specifically asked when a multisensory event with asynchronous stimuli is perceived.

In a variant of the temporal bisection task, participants were asked to estimate whether the second stimulus, in a sequence of three, was presented closer in time to the first or the third stimulus (Burr, Banks, & Morrone, 2009). In order to investigate whether the perceived time of the auditory or visual stimuli is attracted towards one another, temporal conflict was introduced for the first and the third stimulus pair. An auditory stimulus was either leading for 80 ms, lagging for 80 ms, or presented in synchrony with the visual stimulus. The second stimulus was an audio-visual stimulus with no conflict. Results showed auditory dominance in the task, and the perceived time of audio-visual stimuli with a temporal conflict was biased towards the time of the auditory stimulus. In another study, an audio-visual stimulus was presented in the background of a pure tone, 1250 ms in duration (Hartcher-O'Brien & Alais, 2011). Participants were asked to estimate whether a brief audio-visual stimulus was presented before or after the middle of

the background tone. As in the previous study, the perceived time of the audio-visual stimulus with temporal conflict was biased toward the presented time of the auditory stimulus. These findings indicate auditory dominance in perceive time of multisensory event. However, it is possible that the task designs affected this strong bias. For example, in the later study, the presented time of the audio-visual stimulus was estimated relative to the background auditory stimulus. It is possible that this design biased participants towards timing of the auditory stimulus. In order to quantify the shifts in perceived time of unisensory signals (see Figure 1.1) when presented in temporal proximity of signal from another modality, Vidal (2017) sequentially presented four pairs of auditory and visual stimuli, followed by the fifth, unimodal stimulus (visual or auditory). In separate blocks, participants were asked to estimate the rate of either visual or auditory stimuli. Asynchrony between the signals was varied, and a large range of asynchronies was tested (up to 200 ms). The task was to respond as to whether the unisensory stimulus was presented sooner or later, relative to the regular rhythm presented by the first four events. The study provided several important insights. First, temporal ventriloquism is asymmetric. Perceived time of a visual stimulus was biased towards time of auditory stimuli, and the opposite effect was very small. Second, the effect depended on the order between visual and auditory stimuli. More specifically, the perceived time of the visual stimulus was affected to a greater extent if the auditory stimulus was presented after the visual (visual stimulus perceived later). Importantly, this study showed that when signals are appropriately matched in their reliabilities, there is symmetrical attraction between modalities, thus contradicting previous results. It should be noted that in order to reduce transfer effects from previous trials, asynchronous audiovisual pairs were presented four times on each trial, before the unisensory target. Although repetition of the audio-visual stimuli with the fixed SOA in each trial reduced effects of previous trials on the perceived time of multisensory events, it could induce fast recalibration (van der Burg, Alais, & Cass, 2018). In particular, since the same asynchrony was presented multiple times, fast adaptation could lead to an overestimation of the ventriloquist effect in this study.

### 1.2.1.3 Multisensory duration perception

Perceived duration is affected by multisensory interactions, with similarities to perceived time of events. For example the perceived duration of the visual stimuli is affected by the durations of irrelevant auditory stimuli that partially overlap in time (Klink, Montijn, & van Wezel, 2011). The effect is asymmetric: auditory durations affect visual estimates more than visual durations affect the perceived



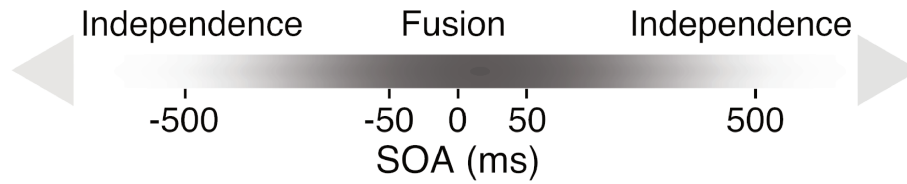


FIGURE 1.1: Illustration of interactions between two modalities as a function of temporal delay. When the delay is very small, the two events are fused, and a single, multisensory event is perceived. For very large temporal delays between signals, there is no interaction between the two signals. Between the two extremes, there is a range of delays within which perceived time of events is affected by the time of the other event. Adapted from Vidal (2017)

duration of an auditory stimulus. The magnitude of the conflict is an important factor for interactions, since auditory durations that are too different from visual durations do not change performance. Intersensory auditory grouping reduces the effect of auditory duration on visual, indicating a preference for intrasensory, over multisensory, interactions.

The first studies investigating multisensory combination of perceived durations did not show an improvement on duration discrimination tasks for multisensory relative to unisensory stimuli (Eijkman & Vendrik, 1965; Walker, Irion, & Gordon, 1981). When asked to reproduce durations of visual, auditory or bimodal durations, in the range of 1 to 1.5 seconds, auditory dominance was observed. However, the dominance was eliminated by reducing the intensity of the auditory stimulus (Walker et al., 1981). Auditory dominance is not always observed, and the perceived duration of auditory stimuli can also be affected by the duration of visual stimuli (van Wassenhove, Buonomano, Shimojo, & Shams, 2008).

#### 1.2.1.4 Adaptation to asynchrony

Repeated exposure to asynchronous auditory and visual stimuli leads to adaptation, and recalibrates the perceived temporal relationship between stimuli (Fujisaki, Shimojo, Kashino, & Nishida, 2004; Vroomen, Keetels, De Gelder, & Bertelson, 2004). After repeated exposure to a visual stimulus lagging for 235 ms, synchrony judgements were shifted in the direction of the adapted lag, and a visual stimulus lagging the auditory for about 30 ms was estimated to be synchronous with the auditory stimulus.

The effect was found with different tasks (Fujisaki et al., 2004; Vroomen et al., 2004), and stimuli (Fujisaki et al., 2004; Navarra et al., 2005; Vatakis et al., 2007). The magnitude of adaptation depends on the SOA between the audio-visual pairs (Roach, Heron, Whitaker, & McGraw, 2011). The adaptation effect is about 10% of the adapted lag, and the effect is robust (Navarra, García-Morera, & Spence, 2012;

Roseboom & Arnold, 2011; Roseboom, Kawabe, & Nishida, 2013; van der Burg, Alais, & Cass, 2015; Yarrow et al., 2011). After adaptation to an audiovisual lag, changes in sensitivity of discrimination and shifts in the transducer function for synchrony discrimination are found (Roseboom, Linares, & Nishida, 2015). These two effects are considered hallmarks of sensory adaptation, suggesting that the effect is perceptual, rather than decisional (Roseboom et al., 2015). Therefore, adaptation to asynchrony shows the same characteristics as adaptation to low level, non-temporal attributes (such as orientation). Spatial congruency is an important factor for recalibration (Yarrow et al., 2011; Yuan, Li, Bi, Yin, & Huang, 2012). Moreover, it is possible to simultaneously adapt to two different temporal relations (auditory stimulus first or visual stimulus first), if adaptors are presented at different locations in the visual field (Heron, Roach, Hanson, McGraw, & Whitaker, 2012; Roseboom & Arnold, 2011).

Even single exposure to asynchrony can lead to recalibration (van der Burg, Alais, & Cass, 2013), although it seems to be specific to audio-visual pairs (van der Burg, Orchard-Mills, & Alais, 2014). The effect of rapid calibration is asymmetric, and more pronounced if the visual stimulus is presented first (van der Burg et al., 2013).

Transfer of adaptation across the senses is an important tool for assessing whether the processing of temporal information in different modalities is conducted by a single or multiple mechanisms. Few studies investigated whether changes in temporal order after adaptation to asynchrony between two modalities (e.g. vision and audition) transferred to other modality pairs (Di Luca, Machulla, & Ernst, 2009; Hanson, Heron, & Whitaker, 2008; Harrar & Harris, 2005, 2008). However, the results are not clear, as transfer is sometimes found (Di Luca et al., 2009; Hanson et al., 2008; Levitan, Ban, Stiles, & Shimojo, 2015) and sometimes not (Becker & Rasmussen, 2007; Harrar & Harris, 2005, 2008; Motala, Heron, McGraw, Roach, & Whitaker, 2018). Different hypotheses are proposed to explain the mechanism of recalibration (Vroomen and Keetels, 2010). The first hypothesis is that adaptation to asynchronous events leads to changes in unisensory signal latencies. Support for the latency changes comes from studies which showed transfer of adaptation across sensory pairs (Di Luca et al., 2009; Hanson et al., 2008), as well as decreased reaction time (Navarra, Hartcher-O'Brien, Piazza, & Spence, 2009), although these effects are not always found (Yuan et al., 2012). In addition, the phase of neural oscillations can code the perceived time of events, and the phase shifts with the change in perceived time following adaptation (Kösem, Gramfort, & Van Wassenhove, 2014). According to the second account, changes in reported simultaneity are caused by changes in the criterion for simultaneity, rather than changes at the

sensory level. This hypothesis is not in agreement with findings showing that after adaptation to asynchrony both a lateral shift in the transducer function as well as a change in sensitivity are observed (Roseboom et al., 2015). These results give strong support to adaptation having a sensory origin. The third hypothesis assumes that there is a network of neurons tuned to different asynchronies (analogous to orientation tuned cells in visual cortex, for example). Repeated exposure to certain asynchrony changes the gain of cells tuned to that asynchrony, resulting in repulsive effects from the adaptor (Roach et al., 2011). Yarrow, Minaei, and Arnold (2015) made explicit predictions from these three hypotheses and conducted an adaptation experiment to assess which model accounts for the data best. Results of their experiment on a group level gave support to latency and criterion shift hypotheses, rather than the population-code model.

#### **1.2.1.5 Adaptation to perceived duration**

Exposure to a certain duration changes the perceived duration of stimuli of the same modality (Walker et al., 1981). In addition, no cross-modal transfer is found (Walker et al., 1981). In a human neuroimaging study, the effects of adaptation to a duration of a visual stimulus were found in the right inferior parietal lobule (Hayashi et al., 2015). Importantly, the effect was specific to duration, since repeated presentation of a non-temporal attribute (shape) did not elicit activation in the same locus.

Adaptation to multisensory duration was used to investigate the hierarchical relationship between multisensory combination and temporal estimation (Heron, Hotchkiss, Aaen-stockdale, Roach, & Whitaker, 2013). More specifically, Heron et al. (2013), presented participants with temporally overlapping auditory and visual stimuli. They found that when durations of auditory and visual stimuli were discrepant, the visual duration was attracted towards the duration of the auditory event. However, when multisensory stimuli containing conflict were used as adaptors, the effect of adaptation was consistent with adaptation to the physical, and not the biased visual estimate. These results are consistent with early encoding of duration that precedes multisensory integration.

#### **1.2.1.6 Modelling multisensory integration**

A very strong hypothesis of how the brain combines multiple sources of information is the modality appropriateness hypothesis (Welch & Warren, 1980). According to this hypothesis, different senses are dominant for encoding different

attributes. For example, audition is superior for the encoding of temporal information, whereas vision is superior for the encoding of spatial information. Therefore, when presented with a temporal conflict between the two unisensory signals, perceived time will be dominated by the timing of the auditory information. Although results of multisensory cue-combination experiments made this hypothesis very unlikely, there seem to be some conditions in which auditory dominance is reported (Burr et al., 2009).

### **Maximum likelihood estimation for cue combination**

The maximum likelihood estimation (MLE) model of multisensory integration proposes that signals from different modalities are combined in a statistically optimal manner. The model predicts that the final estimate will be a weighted sum of the two unisensory estimates, weighted by their reliabilities.

Integrating different cues in this manner yields estimates that have reduced uncertainty compared to unisensory signals.

A great body of work found that unisensory cues are combined according to the MLE rule both between (Alais & Burr, 2004; Ernst & Banks, 2002; Gepstein & Banks, 2003) and within sensory modalities (Hillis, Watt, Landy, & Banks, 2004; Knill, 2003; Landy & Kojima, 2001). There is evidence, however, that when cues from different modalities are combined, information from individual cues is not lost (Hillis, Ernst, Banks, & Landy, 2002a), suggesting crucial difference between cue combination between and within modalities.

An advantage of the MLE rule over the modality appropriateness hypothesis (Welch & Warren, 1980) is its flexibility. More specifically, signals from different modalities are always combined, but since they are weighted by their reliability, the final estimate will be biased more towards the more reliable signal. However, the MLE model is appropriate only for relatively small discrepancies between signals. As asynchrony between the two signals increases, the MLE will no longer be appropriate, and the two signals will not be integrated. The two signals can still bias the perceived time of the signal in the other modality, even for larger asynchronies, as discussed in the previous section (Roach, Heron, & McGraw, 2006; Vidal, 2017).

Studies of temporal ventriloquism raise the question of whether the MLE rule can be applied to model the temporal integration of multisensory signals. More specifically, studies in which temporal conflict was presented between auditory

and visual signals, found auditory dominance beyond that predicted by signal reliability (Burr et al., 2009), and reliability of the combined estimate did not correspond to the predicted reliability following the MLE rule (Burr et al., 2009; Hartcher-O'Brien & Alais, 2011).

Roach et al. (2006) showed that perceived rate was biased towards the rate of the other modality, even when participants were asked to attend to only one modality. When the uncertainty of estimates was matched for the two modalities, multisensory interactions were found for both auditory and visual rate estimation. Furthermore, they tested a large range of conflicts between rates, and found that the strength of multisensory interactions varied with the size of the conflict. They proposed a Bayesian model to account for the data. In addition to the combination of likelihoods weighted by their reliability, a prior that reflects the probability of the two modalities having the same source is proposed. The final estimate of the perceived rate is a product of the weighted sum of the signals as well as the prior knowledge about correspondence between the two signals.

### **Causal inference**

It has long been noted that the brain has to solve the problem of whether two signals reaching two senses have the same cause or not (correspondence problem). To do so, different cues can be used, such as spatial and temporal proximity. The causal inference model proposed by Körding et al. (2007) and Sato, Toyoizumi, and Aihara (2007), formalizes the manner in which brain can solve the correspondence problem. In the causal inference model of multisensory cue combination, the brain both estimates the attributes of interest (e.g. spatial position of auditory and visual signals), as well as whether the two estimates have a common cause. The likelihood of unisensory signals is combined with a prior probability of the two events having the same cause. Based on the estimate of the common cause, signals are either integrated or not. The model was successful in explaining data from spatial localization experiments, as well as explicit judgements about the common cause between spatially disparate events (Körding et al., 2007; Sato et al., 2007). However, the prior probability that two events have the same cause is a free parameter in the model. In order to understand and predict multisensory interactions in different tasks, we need to investigate which cues underlie the prior expectation, and how they vary with the context. For example, in a rate-discrimination task of audio-visual stochastic sequences, judgements of a common source of auditory and visual signals depend on pattern similarity and the maximum temporal offset between the two signals (Locke & Landy, 2017).

## 1.2.2 Effects of temporal context on perceived time

In this section I will review findings that demonstrate how temporal context of stimuli affects temporal estimates.

### 1.2.2.1 Time shrinking illusion

When an empty interval between two events (target) is presented after another shorter interval (distractor), the perceived duration of the target interval is underestimated (Nakajima, Hoopen, Hilkhuysen, & Sasaki, 1992; Suetomi & Nakajima, 1998). This *time shrinking* effect is found for both auditory and visual stimuli, and depends on the duration of the target interval (Arao, Suetomi, & Nakajima, 2000). Temporal assimilation or regularization are proposed to explain the bias (Sasaki, Nakajima, & Hoopen, 1998; Sawai, Sato, & Aihara, 2012). Burr and colleagues further investigated generalization of this effect to a wide range of durations. In addition, they tested perceived durations between auditory, visual and tactile stimuli (Burr, Della Rocca, & Morrone, 2013). They found that distractors affected the perceived duration of the target interval, but for durations of the target shorter than 500 ms. The effect was also found for distractors presented after the target interval, indicating that the locus of the effect can be in later processing stages. Finally, the contextual effect was greater for intervals that were estimated with greater uncertainty. In addition to bias, thresholds for discrimination of brief visual events are also affected by other stimuli preceding them (Karmarkar & Buonomano, 2007a; Spencer, Karmarkar, & Ivry, 2009a). More specifically, thresholds are elevated for the discrimination of intervals that are preceded by distractors, but only in blocks in which the presentation time of the distractor relative to the target duration was variable (Karmarkar & Buonomano, 2007a). In addition, the effect was found only when interval between the distractor and the first target was similar to the estimated duration; when distractor intervals were less similar to the target duration, no difference was found between variable and fixed distractors (Spencer et al., 2009a).

### 1.2.2.2 Debut effect

When visual stimuli are presented in a sequence, the duration of the first stimulus is overestimated up to 50%. The effect was termed *debut* illusion, since it is the perceived duration of the first stimulus that is subject to the dilation. The effect does not depend on the interval between stimuli presentation, contrast or size of

the stimuli (Pariyadath & Eagleman, 2007; Rose & Summers, 1995). Given that the effect is not affected by low level dimensions of the stimuli (Rose & Summers, 1995), it is possible that it does not have an early locus. In addition, the illusory duration dilation does not occur for auditory stimuli (Rose & Summers, 1995).

A phenomenon related to the debut illusion is the subjective overestimation of perceived duration termed *chronostasis* or the *stopped clock* illusion (Yarrow, Haggard, Heal, Brown, & Rothwell, 2001). The illusion was initially described as an illusory dilation of the duration of changing targets, such as the hand of a clock, presented at the landing position of a saccade. In a more thorough investigation of the illusion, Yarrow et al. (2001) asked participants to saccade to a counter. The counter displayed 0 before the saccade, and at the saccade onset the display changed, and the digit 1 was shown when participants foveated the counter. The duration of the first digit shown after fixation was varied, and followed by presentation of 4 successive digits that were presented for a fixed and equal duration. Participants compared the duration of the first variable stimulus to that of the fixed references. In line with the stopped clock illusion, it was found that the perceived duration of the first number after the saccade was overestimated (Yarrow et al., 2001, 2011). In addition, in an audiovisual temporal order judgement task, a sound had to be presented earlier during the saccade in order to be perceived as simultaneous with the moment the postsaccadic target was perceived (Yarrow, Whiteley, Haggard, & Rothwell, 2006). Interestingly, the bias was proportional to the size of the saccade, and the larger the saccade, the larger the overestimation of duration (Yarrow et al., 2001). This relationship is interpreted as the evidence for a hypothesis that the period of impaired vision during the saccade is compensated at the end of the saccade. More specifically, the duration of the saccade is added to the duration of the stimulus presented after the eye movements (Yarrow et al., 2001, 2011). An effect similar to the visual chronostasis was found for shifts in attention between the signals presented in the two ears (Alexander, Thilo, Cowey, & Walsh, 2005; Hodinott-Hill, Thilo, Cowey, & Walsh, 2002). The chronostasis effect in audition provides evidence against the hypothesis that temporal distortions are the consequence of a compensation of saccade duration. Similarly, when the arm is moved to a vibro-tactile target, the duration of the stimulus is also overestimated, relative to the subsequent stimuli (Yarrow & Rothwell, 2003). Although these phenomena have similar perceptual effects, it is not clear whether there is the same underlying mechanism.

### 1.2.2.3 The perceived duration of overlapping intervals

In our environment, events usually have onsets and offsets that overlap in time. Not surprisingly, estimating duration of overlapping intervals is more difficult than that of a single interval (Ayhan, Revina, Bruno, & Johnston, 2012; Cheng, Yang, Han, Ding, & Fan, 2014; de Montalembert & Mamassian, 2012). Moreover, when two durations overlap in time, the duration of the second interval is overestimated (Bryce & Bratzke, 2016; de Montalembert & Mamassian, 2012; van Rijn & Taatgen, 2008). The longer the interval between the onset of the first and the second stimulus, the larger the overestimation (Bryce & Bratzke, 2016; van Rijn & Taatgen, 2008).

In addition, when the short duration is nested in the longer duration presentation, the long interval was underestimated. The bias is a function of the onset of the short interval (Bryce & Bratzke, 2016). The perceived duration of the short interval was not affected by its location relative to the long interval.

The timing of multiple intervals was initially explained by proposing that multiple parallel timing mechanisms are employed for the estimation of each of the intervals (Ivry, 1996). However, this account cannot explain results obtained with nested intervals (Bryce & Bratzke, 2016). Alternatively, the effects could be explained by a single mechanism, that codes the duration of each segment of overlapped intervals separately. To obtain the final estimate of the presented intervals, the estimates of different segments are combined (Bryce & Bratzke, 2016; van Rijn & Taatgen, 2008). In addition, each segment is weighted, and weights are determined based on segment recency. It would be interesting to investigate whether the weighting and combining the durations has a cost in decision time. In summary, these findings indicate that timing multiple durations is demanding, and that induced biases of perceived duration (Bryce & Bratzke, 2016). The manner in which the perception of overlapping intervals is implemented is an important question that models of temporal processing should account for.

### 1.2.2.4 Recalibration to temporal context

Vierordt's law (1898), or regression to the mean, is one of the well known principles of time perception (and magnitude estimation in general). In particular, temporal estimates are biased: short durations are overestimated, and long durations are underestimated. Estimates of duration depend on the width (Miyazaki, Nozaki, & Nakajima, 2005) and the mean (Jazayeri & Shadlen, 2010) of the range of presented durations. Furthermore, the bias depends on the variability of estimates. In



particular, it is greater in blocks with longer durations, which are assumed to be estimated with greater variability (Gibbon, 1977; Jazayeri & Shadlen, 2010; Miyazaki et al., 2005). A Bayesian model was proposed to account for the recalibration to the temporal context. In the model, the likelihood of a temporal estimate is combined with a context-dependent prior. Combining the prior with the encoded duration induces the bias, which is more pronounced for durations that are longer, and encoded with greater uncertainty (Jazayeri & Shadlen, 2010). This strategy optimizes the tradeoff between bias and variability (Mamassian & Landy, 2010). In addition, participants can easily learn different prior distributions (Acerbi, Wolpert, & Vijayakumar, 2012; Roach, McGraw, Whitaker, & Heron, 2017).

### 1.2.2.5 Duration adaptation

A series of studies reported that humans can adapt to interval duration (Becker & Rasmussen, 2007; Curran, Benton, Harris, Hibbard, & Lee, 2016; Heron, Aaen-Stockdale, et al., 2012). After repeated exposure to a fixed duration (*adaptor*), the perceived duration (*test*) is repelled away from the adaptor duration (Heron, Aaen-Stockdale, et al., 2012). This repulsion resembles negative after-effects in adaptation studies, such as adaptation to orientation or color. Consistent with these findings is a hypothesis that perceived duration is mediated by duration sensitive channels (Heron, Aaen-Stockdale, et al., 2012; Walker et al., 1981). According to this model, durations are perceived via sensory-specific and narrow range channels, centered on the preferred duration.

In the study demonstrating duration adaptation after-effects, participants adapted to a duration of visual or auditory stimuli, by repeated exposure to a fixed duration of a visual Gaussian blob or auditory white noise. Then, their task was to compare the duration of the reference duration, presented in the other modality, with test duration in the same modality as the adaptor. Adaptation had an effect on the perceived duration, and adaptation to longer durations reduced the perceived duration of the test stimulus, for durations between 160 and 640 ms. The effect was tuned in time, and adaptation was found only when the adaptor and the test durations had similar durations. Duration after-effects are broadly tuned (Fulcher, Heron, McGraw, Roach, & Whitaker, 2016). Moreover, duration after-effects transfer across visual hemifields (Li, Yuan, & Huang, 2015), and up to 15 degrees of visual angle (dva) (Maarseveen, Hogendoorn, Verstraten, & Paffen, 2017), suggesting a late locus of adaptation.

A model of duration tuned channels that selectively adapt to different durations

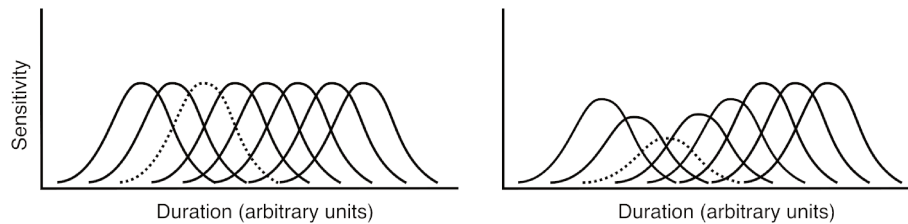


FIGURE 1.2: Illustration of adaptation to a fixed duration in the duration channel model. Model tuning curves before (left) and after (right) adaptation to a fixed duration. Adapted from Heron, Roach, et al. (2012)

(Figure 1.2.) was proposed (Heron, Aaen-Stockdale, et al., 2012). In the channel-based model processing of duration is realised by neurons tuned to different durations (or lags) (Fulcher et al., 2016; Heron, Roach, et al., 2012; Roach et al., 2011). The level of activation of each unit depends on the extent to which the presented duration is similar to its preferred duration. Adaptation is explained by a change in the sensitivity of the units, due to repeated exposure of a fixed duration, that a certain number of units are responsive to. A difficulty for the channel-based model applied to duration encoding comes from the unidirectionality of time. More specifically, since duration unfolds in time, all duration channels up to a given duration will be activated. This difficulty could be avoided by a coincidence detection mechanism, that codes for stimulus onset and offset (Van Wassenhove & Lecoutre, 2015). In addition, a recent study found that adaptation to duration depends on factors that are not predicted by the duration channel model. For example, when adapting to a random dot kinematogram, adaptation reduced perceived duration of the test stimulus, regardless of the duration of the adaptor (Curran et al., 2016). The duration population models are supported by evidence showing that there are duration selective cells in early auditory and visual cortices (Brand, Urban, & Grothe, 2000; Casseday, Ehrlich, & Covey, 1994; Ehrlich, Casseday, & Covey, 1997; Eriksson, Tompa, & Roland, 2008; He, Hashikawa, Ojima, & Kinouchi, 1997). One human neuroimaging study investigated the neural correlates of duration adaptation, and found evidence for adaptation-related changes in activation of the inferior parietal lobule (IPL) (Hayashi et al., 2015). More specifically, after repeated exposure to the same duration (but not to the same shape) was related to increase in activity in IPL. Moreover, a recent finding provided evidence for chronotopic maps in human premotor cortex (Protopapa, Hayashi, Kulashekhar, & Zwaag, 2018). In the same study, authors found comparable activation of the same regions in a temporal and orientation judgement task, indicating that the activation was not task specific. Although authors argue that chronotopy reflects duration tuned units, to further understand how activation of these maps correlate with perceived duration, it would be interesting to investigate whether observed maps are robust to

contextual effects (Jazayeri & Shadlen, 2010).

#### 1.2.2.6 The effects of adaptation to flicker/motion

Adaptation to flicker or motion can induce a spatially localized compression of perceived duration, suggesting distinct, local components of the timing mechanism (Johnston, Arnold, & Nishida, 2006). During the adaptation phase, participants were presented with In this paradigm. In the test phase, they reported whether durations of stimuli presented at the adapted location were longer or shorter than those presented at non-adapted locations. The frequency of the adaptor drift was 5 or 20 Hz, and the frequency of the test 10 Hz. After adaptation to 20 Hz motion, perceived duration of a stimulus presented at the adapted location was compressed. An adaptor drifting at 5 Hz had smaller effect on the perceived duration in the same direction. This asymmetry dissociated the aftereffect from frequency adaptation, that is present for both fast and slow adaptors.

The effect of adaptation is not sensitive to differences in orientation of the adaptor and test (Johnston et al., 2006), and it is narrowly tuned in space (Ayhan, Bruno, Nishida, & Johnston, 2009). Whether adaptation is retinocentric and/or in real-world coordinates is not clear. Two different groups of researchers found surprisingly different effects with respect to coordinates of adaptation (A. Bruno, Ayhan, & Johnston, 2010; Burr, Tozzi, & Morrone, 2007). The methods used in the two experiments were somewhat different, notably in the manner in which they accounted for perceived speed after-effects, and the order of stimulus presentation. However, it is not obvious why these differences would lead to opposite results. In addition, the effect does not transfer across eyes (A. Bruno et al., 2010) and isoluminant stimuli do not elicit the effect (Ayhan, Bruno, Nishida, & Johnston, 2011). Moreover, adaptation to fast flicker (50-60 Hz) also induced adaptation effects (Johnston et al., 2008). These findings suggest early locus of the effect, that is possibly mediated by the magnocellular pathway (Johnston, 2010).

To explain the effects of adaptation to high frequency flicker, a content-dependent clock was proposed (Bruno et al., 2011; Johnston, 2010). Based on the evidence supporting the hypothesis of the magnocellular contribution to adaptation, the model proposes that the magnocellular signal is used to predict local image brightness. The prediction is stored and cross-correlated with information encoded in the parvocellular signal. The unit of time is the duration between the two matches between the parvo and magno signals. Adaptation induced phase shift in magnocellular neurons (Benardete and Kaplan, 1999) would shift predictions forward in time, delaying the match between the prediction and encoded information. The delay would result in fewer matches between the predicted and encoded signals,

and a compression of perceived duration. The content-dependent clock in this form is applicable only for duration perception of events, and cannot explain how elapsed duration between two successive events is perceived. Nevertheless, it demonstrates how time mechanisms can employ sensory systems to extract temporal information.

### 1.2.3 Spatial interactions and perceived time

#### 1.2.3.1 The kappa effect: spatial layout affects perceived duration

Temporal estimates between two spatially disparate event increases as a function of spatial separation between those events (Cohen, Hansel, & Sylvester, 1953). More specifically, the duration between a first and second light (larger spatial distance) will be perceived as longer than between the second and third (smaller distance). The kappa effect was found for both vertically and horizontally oriented spatial sequence (Cohen et al., 1953). Also, the effect depends on the perceived distance between the sources of light, rather than physical distance (Lebensfield & Wapner, 1968), and it is more pronounced for temporal judgements near threshold (Henry & McAuley, 2009). The effect is usually interpreted by the interpolation of motion (velocity) hypothesis (Henry & McAuley, 2009). Perceived temporal intervals are weighted averages of the physical duration of the intervals and the expected time based on the assumption of constant velocity (the ratio of the distance between consecutive lights and the duration between them).

#### 1.2.3.2 Asynchrony across space: spatial layout affects asynchrony thresholds

The relation between the perception of asynchrony and spatial position has been researched in several studies (Forte, Hogben, & Ross, 1999; Motoyoshi, 2004). Motoyoshi (2004) presented a quadruple of flickering gratings with changing orientation. Participants' task was to detect a temporal deviant: one of the four stimuli that changed orientation asynchronously relative to the other gratings. Stimuli were either adjacent or separated by 1 dva. Spatial separation affected thresholds: an increase in spatial distance between events increased asynchrony discrimination thresholds. Furthermore, the effect is asymmetric, and participants are more sensitive in detecting that one event is presented before the other stimuli than that it is presented later. These findings are explained by proposing that the detection of asynchrony across the visual field is carried on by interaction between local orientation detectors. The larger the distance between the detectors, the more noise in their interaction, and more elevated the thresholds. Hess and Maehara (2011) found increased thresholds for detecting an asynchronous stimulus in a quadruple,

for stimuli presented in a circle radius 1 dva (67 ms) than 5 dva (91 ms). Therefore, the effect is found even for large spatial separation between stimuli.

A related question is whether the temporal integration window is different across the visual field. Sensitivity for double pulse detection varies across the visual field (Poggel, Treutwein, Calmanti, & Strasburger, 2006). Poggel et al. (2006) asked participants to detect one stimulus in an array of nine, whose presentation was briefly interrupted. One stimulus was always presented at the fixation, and the rest were presented on a circle of varying radius (from 2.5 to 20 dva). In separate blocks, thresholds were measured at each of the nine positions (one foveal and eight peripheral). In order to detect the gap in the stimulus, the gap had to be 40 ms long if stimuli were presented at 2.5 dva eccentricity and 60ms if stimuli were presented at 20 dva radius. Importantly, foveal thresholds, assessed for each radius size (eccentricity) also increased as a function of radius size. The increase in thresholds for the foveal stimuli was comparable to that of the eccentricity. Therefore, authors concluded that the negative relationship between sensitivity and eccentricity is due to the difference in the size of attentional focus.

### 1.2.3.3 Perceived time and position in the visual field

Temporal processing is not homogeneous across the visual field. For example, visual flicker is more salient in the periphery (Porter, 1902). However, early studies of temporal resolution across the visual field showed little difference in TOJ and SJ thresholds (McKee & Taylor, 1984; Westheimer, 1983). Recent studies showed that the perceived duration of a stimulus, as well as a duration between two brief visual stimuli, are perceived as shorter in the periphery than at the fovea (Aedo-Jury & Pins, 2010; Kliegl & Huckauf, 2014). In particular, perceived duration at larger eccentricities was compressed relative to stimuli presented at the fixation, for durations marked by stimuli designed to elicit responses primarily in the magno-pathway. There were no effects for parvo-based stimuli (Aedo-Jury & Pins, 2010). In addition, the effect of eccentricity was not eliminated by scaling the size of the stimuli to match cortical representations (Kliegl & Huckauf, 2014) or matching the visibility of stimuli (adjusting the contrast and size of the stimuli so that reaction time to stimuli presented at different positions is the same) (Aedo-Jury & Pins, 2010).

## 1.3 Models of duration perception

It is a fundamental question whether the plethora of different timing behaviours is mediated by a single central mechanism, or multiple distributed mechanisms. The first models of temporal processing already recognized that a single mechanism could not feasibly account for timing on multiple time-scales (Treisman, 1963). A great number of models have been proposed since then. Before reviewing some of the most influential models I will briefly discuss behavioral data that provided insights into this question.

### 1.3.1 Time Mechanism: Centralised or Distributed?

Human behavior is organized in timescales that span from milliseconds to days, and it is probable that they are not mediated by the same mechanisms. Speech perception and production, as well as motor control, require processing of time on the milliseconds scale (Mauk & Buonomano, 2004), while longer durations are needed for learning (Gallistel, 2011; Gallistel & Gibbon, 2000), decision making, and organization of episodic memories (Eichenbaum, 2015). I will present different lines of research that provide insights into important distinctions between different timing mechanisms.

Evidence from studies investigating time perception in humans that are isolated from environmental inputs showed important dissociations. For example, estimating passage of time during the day requires synchronization with external rhythms, and it is affected by isolation (Aschoff, 1998). On the other hand, it is unlikely that the discrimination of very brief duration is affected by a lack of synchronization of circadian clocks with the environment (Lewis, Miall, Daan, & Kacelnik, 2003; Pöppel, 1997), although there is some evidence to the contrary (Agostino, Do Nascimento, Bussi, Eguía, & Golombek, 2011). These studies are important, since they show that even when separated from external rhythms, human temporal mechanisms can still function, although altered for durations in a certain range.

One way of investigating whether time is represented in the same way (and by the same mechanisms) for different range of durations is to investigate whether variability of estimates scales in the same way across different durations. One of the hallmarks of time perception is linear scaling of variability with the duration of the estimated interval (Allan, 1979; Allan & Gibbon, 1991; Church, 1984; Gibbon, 1977; Treisman, 1963; Westheimer, 1999). In time perception, this increase of variability with duration to be time is referred to as *scalar variability of timing*. It is, in fact, an application of the Weber's law for time perception: the ratio of the change

in stimulus needed to detect the change and the magnitude of the stimulus is constant (Solomons, 1900). There are two forms of this law in the time perception research: the original and the generalized form (Bizo, Chu, Sanabria, & Killeen, 2006; Grondin, 2012). The generalized form acknowledges that the variability of the estimate includes both on the stimulus magnitude and a constant component. Therefore, depending on the magnitude of this non-temporal variability and the duration of the interval to be estimated, the coefficient of variation need not necessarily be constant across the durations. There is conflicting evidence regarding conformity to this law for different duration ranges and tasks (Allan, 1979). For example, it seems that the variability of estimates for durations under 100 ms is disproportionately larger than predicted (Burr et al., 2013; Tiest & Kappers, 2009). In a study testing temporal reproduction of durations spanning from 68 ms to 16.7 minutes, no evidence for a clear break point was found (Lewis & Miall, 2009). However, as the authors remark, the absence of a break point between suprasecond and subsecond temporal estimation cannot be taken as an evidence against multiple timing mechanisms (Lewis & Miall, 2009).

Human neuroimaging studies showed different correlates of performance in subsecond and suprasecond tasks and gray matter volume (Hayashi, Kantele, Walsh, Carlson, & Kanai, 2014; Lewis & Miall, 2009). When asked to discriminate durations in the subsecond and suprasecond range, different areas were differentially activated (Lewis & Miall, 2009). More specifically, the parietal cortex, pre-supplementary motor area and frontal areas were active during temporal discrimination in both time scales. However, the frontal periculum, left cerebellar hemisphere and temporal gyri showed greater activity during discrimination of shorter intervals (Lewis & Miall, 2009). Another study related performance in temporal discrimination tasks and gray matter volume. For durations in the suprasecond range, the smaller the volume in the inferior parietal lobe, the better the performance, possibly revealing a relationship between the ability to estimate suprasecond durations and working memory and attentional capacity (Hayashi et al., 2014). On the other hand, the ability to discriminate subsecond durations was correlated with volume in the bilateral anterior cerebellum, indicating links between suprasecond timing and the motor system (Hayashi et al., 2014). In addition, pharmacological experiments showed a double dissociation between impairments in estimating durations in the subsecond and suprasecond range (Rammsayer, 1994; Rammsayer & Vogel, 1992). Drugs that disrupt working memory impair performance in the discrimination of temporal intervals in the suprasecond range, but not the subsecond range (Rammsayer, 1994). On the other hand, ethanol injection affects millisecond timing, but not temporal estimates in the suprasecond range

(Rammsayer & Vogel, 1992).

Another way to investigate whether there are one or more mechanisms involved in time perception is to search for correlations between different tasks and stimuli. There is some evidence that the variance of estimated duration in motor and perceptual timing within the subsecond range is scaled with the estimated duration in the same way (Ivry & Hazeltine, 1995). Moreover, a correlation was found between motor timing of different effectors (finger and foot), that suggests that they share a common mechanism (Keele, Pokorny, Corcos, & Ivry, 1985). However, a recent study showed that when the variability in different timing tasks in the visual and auditory modality were correlated across participants, the correlations were greater for performance in the same task, than for performance in different tasks with stimuli from the same modality (Merchant, Zarco, Bartolo, & Prado, 2008).

Transfer or specificity of perceptual learning across tasks, stimuli or modalities also provides evidence for common processing systems. For example, one study showed that after ten days training to discriminate 100 ms 1 kHz tones, thresholds significantly improved (Wright et al., 1997). There was a generalization of learning across frequencies. Most studies investigating temporal perceptual learning confirmed these results (Buonomano, Bramen, & Khodadadifar, 2009; Nagarajan, Blake, Wright, Byl, & Merzenich, 1998; Rammsayer, 1994; Wright & Sabin, 2007). Unlike transfer to other durations, spatial generalization of learning is found in vision (Wertheimer, 1999), and in the tactile modality (Nagarajan et al., 1998). There is also a generalization across modalities (Bueti, Lasonara, Cercignani, & Macaluso, 2012; Nagarajan et al., 1998). The specificity of temporal perceptual learning for trained durations has been used as an argument against a centralized timing mechanism (Bueti & Buonomano, 2014).

It seems, however, that perceptual learning of features that are known to have representations in early cortex, such as orientation, are not necessarily spatially specific (Mastropasqua, Galliussi, Pascucci, & Turatto, 2015; Xiao et al., 2008), correlates of behavioral improvements are not always identified (Ghose, Yang, & Maunsell, 2002; Schoups, Vogels, Qian, & Orban, 2001), and the generalization of perceptual learning can depend on task difficulty (Ahissar & Hochstein, 1997). Therefore, it is difficult to draw conclusions about chronotopy solely from the presence or absence of learning transfer.

In sum, evidence from studies of the perceptual learning of features that are known to have early cortical representations suggests that both specificity and transfer, for feature (orientation) and spatial position, can be found.

Audiovisual simultaneity judgements are also improved with learning, and



there is about 40% reduction in the temporal window of integration after training (Powers, Hillock, & Wallace, 2009). Changes in neural activity were found after perceptual learning of temporal discrimination in both auditory (van Wassenhove et al., 2007) and visual (Buetti et al., 2012) modality.

### 1.3.2 Information Processing Models

The first elaborate model of temporal processing is the information-processing model proposed by Michael Treisman in 1963 (Treisman, 1963). The information processing model (Creelman, 1962; Treisman, 1963) was designed to explain the results of several experiments, which used different methods (reproduction, production and discrimination) and a wide range of durations (0.25 to 9s). These include conformity to Weber's law, regression to the mean of constant errors, lengthening (the longer the session, the longer the produced durations), and serial effects in temporal estimation (Treisman, 1963). According to Treisman (1963), estimated time is a percept, just like perceived color or temperature. The difference between perceived time and attributes such as color or orientation is that there is no sensory organ for perceiving time. Several distinct units with separate functions constitute the temporal mechanism. Temporal information is generated from an internal pacemaker, that emits linearly spaced pulses at a regular rate. Perception of temporal information is achieved by opening and closing a switch between the pacemaker and the accumulator, the unit in which pulses are temporarily stored. Once the event to be timed has elapsed, the number of pulses (units of time) is stored in the memory unit. Decisions are made in the comparator unit, by comparing the accumulated pulses to a threshold. Weber's law arises from correlations of pulses emitted for one estimated duration, and fluctuations in the regularity of pulses between trials (Treisman, 1963). In the first implementation of the model, the pulse rate is not fixed, and can be modulated by arousal. A schematic representation of the model is shown in Figure 1.3.

This pacemaker mechanism was inspired by biological mechanisms, such as pacemaker cells in invertebrates, neural oscillations, and regular body rhythms such as respiratory or heart rate (Treisman, 1963, 2013).

The aim of the proposed model was to account for both perception (more specifically, reproduction of prospective durations), as well as timing of the motor action. Therefore, Treisman proposed multiple pacemakers at different levels in the hierarchy to account for movement timing of different parts of the body. Instead of having a central pacemaker, and separate motor programs, he proposed that it is more efficient to have the same program whose time will be modulated by different pacemakers. Several modifications of the model were introduced later, (Treisman, Faulkner, & Naish, 1992; Treisman, Faulkner, Naish, & Brogan, 1990), notably the concept of a characteristic frequency of a pacemaker. Behavioral and EEG experiments provided some evidence for the existence of a fixed, characteristic frequency, although results are not unequivocal and multiple bands of spectrum were affected by manipulation (Treisman et al., 1992, 1990). Nevertheless, the model is a useful

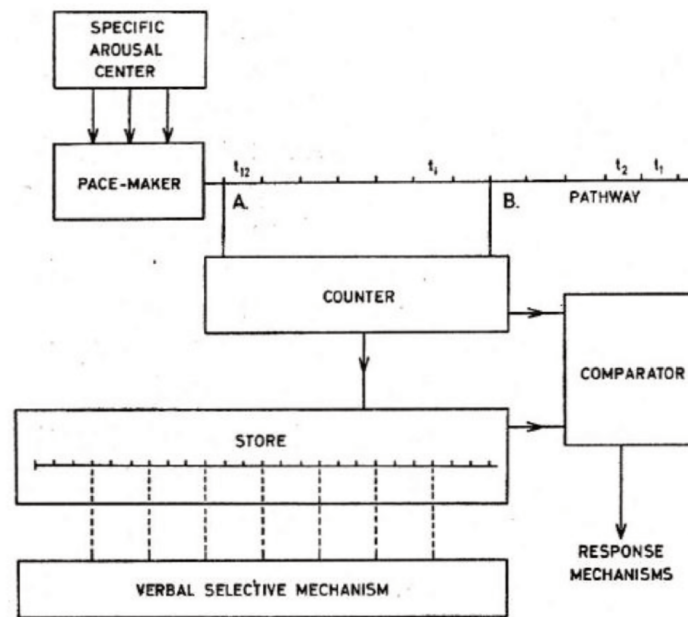


FIGURE 1.3: Information processing model of time perception. Adapted from Treisman (1963)

metaphor to think about time perception, that is still incarnated in many models of perceived duration. More specifically, one common attribute of different dedicated time models is the notion of mandatory resetting of the clock (or activation of the switch).

### 1.3.3 Scalar Expectancy Theory

Scalar expectancy theory (SET) (Gibbon, 1977) was developed to explain how animals develop temporal expectations. It can, however, account for behavior of both humans and animals in several tasks, such as bisection, reproduction or discrimination (Allan & Gibbon, 1991; Gibbon, 1977). The different information that obtained by these measures are discussed in the Section 1.1. There are two main findings that the model accounts for: the proportional timing and scalar property of timing. The proportional timing refers to a linear relationship between the mean latency of the response and the interval between the stimulus and reward. In other words, the longer the duration to be estimated, the longer is the time to response. Scalar property refers to the linear scaling between the variability (standard deviation) of the temporal estimate and the magnitude of the estimate (Allan & Gibbon, 1991; Gibbon, 1977). This model follows the architecture of Treisman's information processing model, with a few distinctions. As in the previously described model, separate units, pacemaker, switch and accumulator are used to estimate interval duration.

Pulses are generated by the pacemaker with a Poisson distribution. Temporal information is coded as expectancy (hope), as the model was developed to explain timing to reward in animals. Another memory storage is included in the model. More specifically, accumulated impulses are stored in short term memory for immediate comparison, while long term, memory stores samples of previous trials. The response is given in a decision stage, where the presented duration from short term storage is compared to the reference duration. In SET, depending on the task (e.g. temporal bisection or discrimination), different comparisons are conducted. It is not clear, however, whether the comparator stage of the model is part of the decision making cognitive mechanism that is employed for discriminations of different attributes, such as color, position and time. The source of scalar variability is in the memory stage, where the accumulated number of pulses is multiplied with the *memory translation constant* (Gibbon, Church, & Meck, 1984). Due to multiplication, the distribution of pulses, which on average have shorter duration, will be narrower than the distribution with a larger mean value.

The model is very influential and supported by various pharmacological studies (Allan & Gibbon, 1991; Meck, 1996), SET has been accused of being unfalsifiable (Staddon & Higa, 1999). In particular, it has a large number of components with rather flexible mechanisms of functioning. Scalar timing theory has a large number of potential parameters, and although few of them are varied to account for the data (Church, 1984), the theory is not explicit as to which parameters could be varied or fixed, and the same effects can be produced by varying parameters for different units. In addition to great flexibility, another issue with the model is that it assumes an accumulation unit with infinite capacities, which is probably not feasible in a biological system (Staddon & Higa, 1999).

### 1.3.4 The Striatal Beat Frequency Model

The Striatal Beat Frequency model extends older ideas about multiple oscillators that oscillate at different frequencies (Church, 1984; Miall, 1989; Treisman, 1963). It is closely related to neurobiological findings and is intended to be a biologically plausible model of duration perception (Matell & Meck, 2004; Oprisan & Buhusi, 2011). Previous models proposed that it is the phase of individual oscillators that encode durations. Therefore, time estimation is possible for intervals as long as the longest period of an oscillator. Although there is some evidence showing that oscillations of periods as long as 60 seconds exist in anaesthetized rats (Ruskin et al., 1999), encoding duration in a single oscillation does not seem optimal (Matell & Meck, 2004; Miall, 1989). A more efficient way of coding temporal information

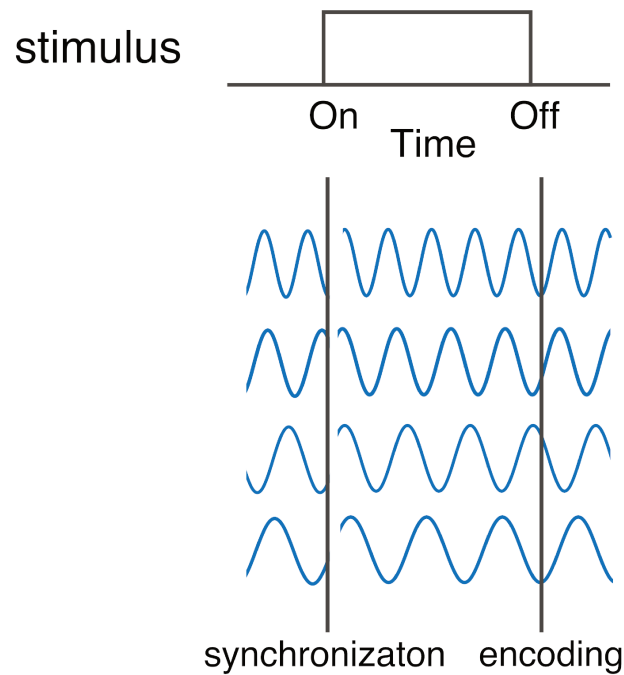


FIGURE 1.4: Illustration of coincidence detection in SBF model. Adapted from Buhusi and Meck (2005)

with oscillating neurons is to detect synchronized activity of multiple oscillators with different frequencies (Matell & Meck, 2004; Miall, 1989; Oprisan & Buhusi, 2011, 2014).

According to the model, at the beginning of the interval to be timed, oscillators are reset to the same phase (Figure 1.4). The encoding of durations is possible by detecting oscillators whose activities coincide in time. Importantly, coincidence detection of oscillators' activity allows for the encoding of durations longer than periods of single oscillators. The Striatal Beat Frequency model extended Miall's ideas by adding noise that is plausible in a biological system, as well as relating oscillations more directly to possible neural correlates (Matell & Meck, 2004). Spiny striatal neurons are proposed as coincidence detectors, and the frontal cortex as the read-out locus. Pharmacological (Matell & Meck, 2004; Meck, 1996) and lesion studies (Malapani & Fairhurst, 2002) indicated that altered functioning of the striatum affects the ability to estimate durations. Neuroimaging studies also confirmed that cortico-striatal structures are necessary for time perception (Coull, Vidal, Nazarian, & Macar, 2004). Computational modeling of a circuit with a large number of input oscillators and a smaller number of output coincidence detectors, showed that scaling of variability with the duration of the interval can arise from noisy storing or retrieval of reference durations (Oprisan & Buhusi, 2011, 2014).

A recent neural network model, based on memory encoding, demonstrated that encoding a single event in the past allows us to decode both the duration and when

the event happened (Maniadas & Trahanias, 2016). The model is based on ideas from the Striatal Beat Frequency model (Matell & Meck, 2004), and assumes that duration is coded by coincidence detection of striatal neurons. The network is able to encode the duration of the an event, by a counting mechanism that increases while the event is presented. In addition, by tracking the evolution of the network even after the event duration has elapsed, information about when an event was presented can be decoded.

### 1.3.5 Intrinsic models of perceived duration

Given the variety of temporal tasks that the brain performs, it has been proposed that encoding time intrinsically in networks processing other aspects of the event, is more appropriate from a computational point of view (Ivry, 1996; Meck & Ivry, 2016; Paton & Buonomano, 2018). In this framework, the circuits involved in the processing of the stimulus also code temporal information, while brain areas shown to be involved in temporal tasks should not be considered centralized timing mechanisms.

The State Dependent Network (SDN) timing mechanism proposes that properties of neurons and synapses that change in time can be used to estimate duration Buonomano (2000). Dynamics of a network depend on the input and the state of the network at the time of the input Buonomano (2000). Output units are trained to read out the dynamics of the network as a temporal information, as shown in Figure 1.5.

In this framework, sensory and motor timing depend on different, non-overlapping networks Buonomano and Laje (2011). Activity of the networks that encode temporal information depends on the sensory input, while motor timing arises from recurrent neural networks that generate self-sustained, time-varying patterns of activity (*population clocks*) Buonomano (2000); Buonomano and Laje (2011). The population clocks model does not have an intrinsic metric of time, although the metric could be learned (Paton & Buonomano, 2018).

The state dependent network model has clear predictions regarding the effect of a distractor on perceived duration. However, these predictions are not always confirmed (Burr et al., 2013; Karmarkar & Buonomano, 2007b; Spencer, Karmarkar, & Ivry, 2009b). For example, Karmarkar and Buonomano (2007b) used a *reset task* to test predictions from the SDN model of time estimation. Participants compared the duration of the target interval marked by two visual events to a fixed, *standard* duration. On half of the trials, another stimulus, the *distractor*, was presented before the target interval. The distractor was presented either at a fixed interval before the

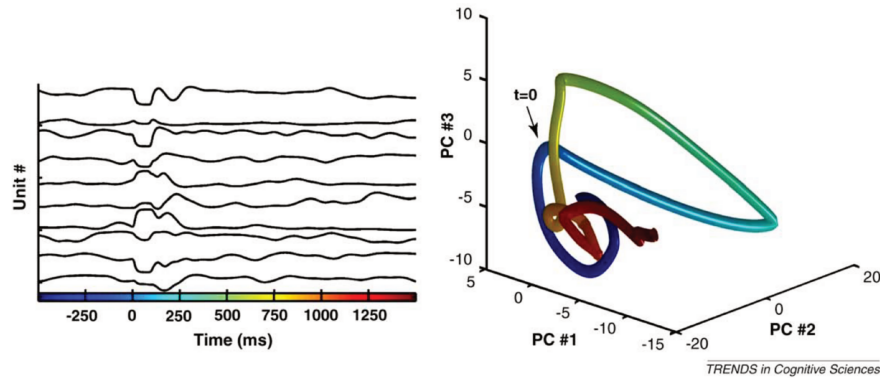


FIGURE 1.5: Illustration of units' trajectory in SDN network. In the left panel, changes in activity as a function time are shown for 10 units of the network. In the right panel, trajectory of the first three principal components is shown. Adapted from Karmarkar and Buonomano (2007b)

target duration, or at a variable time. The constant and variable distractors should have different effects on the state of the network, and therefore interfere differently with the discrimination of the test intervals. Thresholds were indeed elevated for the variable context compared to other conditions. No effect of the constant distractor was found. Given that the variable and constant conditions were tested in separate blocks, it is possible that participants had different strategies for the two conditions. Also, the distractor duration was the same as the duration of the standard which could have confounding effects. When distractor intervals were less similar to the standard duration, and standard durations were longer than 100 ms, there was no difference between the variable and fixed distractors (Spencer et al., 2009b). Furthermore, SDN model cannot explain why presenting the distractor after the target would affect temporal estimation (Burr et al., 2013). Population clocks are a computationally efficient way of encoding temporal information. Behavioral tests of the model predictions suggest that the model could explain temporal estimation in the hundred milliseconds range. For longer durations, the predictions of the model are not supported by the behavioral evidence (Burr et al., 2013; Spencer et al., 2009b).

## 1.4 The encoding of relative time between events

### 1.4.1 The time marker matching hypothesis

The time marker hypothesis of the perception of relative time between events proposes a cross-channel, mid-level, comparison mechanism. This mechanism should explain how temporal relationships are coded, for simultaneity, grouping and binding of attributes and events. The comparison of the temporal order is performed by comparison of time markers associated with salient temporal events. The time markers are amodal, but associated with specific events in time, that could be from different modalities or modules within the same modality (e.g. motion and color). The amodal representation can be a saliency map, that is the extent to which events stand out from the background. Time markers are then related to the salient temporal features of events. The cross-correlation is proposed as a computation underlying the comparison of time markers.

Central to the time marker hypothesis is the idea that they code the moment when an event occurs in the environment, that is different from the moment when processing of the event is completed in the brain. Instead of basing the judgements of relative time on the moment when processing is completed in the brain, the time marker hypothesis proposes that information about event time should be encoded in such a way that it is not biased by different processing times at various stages of processing. Importantly, the perceived time of when an event occurred does not have to be veridical.

Similar to visual motion detection mechanisms, that operate at two levels (O. Braddick, 1974), mechanisms for processing the temporal relation between events might have low-level and mid-level components for processing within-channel and cross-channel attributes, respectively (Nishida & Johnston, 2002). For example, when two visual stimuli are adjoint, the thresholds for detection of asynchrony are extremely low (Victor & Conte, 2002; Westheimer & Levi, 1987). It is probable that thresholds in the order of milliseconds are possible because the asynchrony is detected by motion detectors, indicating that in some conditions perceived asynchrony can correspond to almost physical asynchrony. For cross-channel comparisons, that are either from a different modality or the same modality, but are, for example, spatially disparate, a mid-level mechanism is proposed.

Fast alternations in color and direction of motion are perceived asynchronously. More specifically, changes in color and direction of motion are perceived as simultaneous when the change of stimulus color precedes the change in direction of motion (Arnold & Clifford, 2002b; Clifford, Arnold, & Pearson, 2003; Moutoussis & Zeki, 1997a). This effect was initially explained by different processing latencies for



color and motion (Moutoussis & Zeki, 1997c). According to the time marker matching hypothesis, asynchrony found between motion and color changes (Moutoussis & Zeki, 1997a) is due to a mismatch between temporal markers, rather than processing latencies (Nishida & Johnston, 2002). More specifically, color change is a first-order change. The change of motion direction is a second-order change, and it is only interpreted by the mid-level process. Under fast switching rates between color and motion, the second order changes are unavailable, and the illusion arises because the first order changes are incorrectly matched. It is not clear, however, how the direction of the mismatch is explained (Arnold, 2010).

The time marker hypothesis explains the dissociation between reaction times and temporal order judgements (Cardoso-Leite & Gorea, 2009; Jaskowski, 1996; Tappe et al., 1994), since reaction times reflect the moment when the processing of features of the stimulus crossed some threshold, while temporal order judgements arise from the time marker matching. Furthermore, results of motion transparency (Clifford, Spehar, & Pearson, 2004; Kanai, Paffen, Gerbino, & Verstraten, 2004), synchrony in auditory modality (Arrighi, Alais, & Burr, 2005), and neuroimaging studies of motion-color synchrony (Amano, Nishida, & Takeda, 2004) are consistent with this hypothesis. However, there are findings that are not compatible with the hypothesis (Amano, Johnston, & Nishida, 2007; Arnold & Clifford, 2002b; Linares & López-Moliner, 2006; Viviani & Aymoz, 2001). For instance, there is evidence that the temporal order of perceived motion and color are found for the same order of changes (Moutoussis & Zeki, 1997b; Nishida & Johnston, 2002), and that there is no linear increase of the effect with an increase in the period of oscillations, as the time marker theory would predict (Moutoussis & Zeki, 1997c). Moreover, as the authors note themselves, there can be no solely event time coding in the brain, since at least peripheral processing times will affect the time markers.

#### **1.4.2 How is succession represented in the brain?**

Neural oscillations are spontaneous neural activity, originating from the coherent activity of neural assemblies (Buzsáki, 2010). Neural oscillations can be entrained (Schroeder & Lakatos, 2009; Treisman et al., 1990) or reset (Thorne, De Vos, Viola, & Debener, 2011) by external stimuli. They are categorized in different frequency bands, that are assumed to have different functions in the processing of information (Buzsáki, 2010). The phase of brain oscillations is related to the temporal resolution of the system, and oscillations are hypothesized to serve as chunking and parsing mechanisms (Buzsáki, 2010; Giraud & Poeppel, 2012; VanRullen, 2016; Varela, Toro, Roy John, & Schwartz, 1981). More specifically, it is hypothesized

that oscillations discretize continuous streams of information, and consequently, the two events that fall in the same cycle of the oscillation will be segregated (Giraud & Poeppel, 2012; VanRullen, 2016). In an agreement with this hypothesis, thresholds for successiveness or discrimination of two successive stimuli in the visual (Samaha & Postle, 2015), or auditory and visual (Cecere, Rees, & Romei, 2015; Kristofferson, 1967) modalities are related to the frequency of the alpha rhythm, and correlated across individuals. In addition, performance in segregating two successive flashes of light is related to the phase of alpha oscillations (threshold for succession is around 40 ms), performance in the apparent motion task (inter-stimulus interval needed for elimination of apparent motion is about 120 ms) is related to the phase of theta oscillations (Ronconi, Oosterhof, Bonmassar, & Melcher, 2017).

Interactions between oscillations from different frequency bands can underlie the perceived temporal ordering of events (Buzsáki, 2010; Heusser, Poeppel, Ezzyat, & Davachi, 2017; Lisman & Jensen, 2013). In the temporal domain, the phase shifts of oscillations in alpha band are related to shifts in the perceived time of audiovisual events. These findings are consistent with the hypothesis that slow neural oscillations can serve as temporal reference frames (Kösem et al., 2014; van Wassenhove, 2016). Moreover, the power of prestimulus alpha oscillations is related to the perceived temporal order of audiovisual stimuli (Grabot, Kösem, Azizi, & van Wassenhove, 2017). Transient coupling between theta phase and the power of beta oscillations is found in the temporal anticipation task (Cravo, Rohenkohl, Wyart, & Nobre, 2011), and illusory temporal rate percepts are related to oscillatory activity (Herrmann, Murray, Ionta, Hutt, & Lefebvre, 2016).

In summary, the perception of time is a concept that consists of different and distinct computations, mechanisms and representations (Marr, 1982). The great body of work, both experimental as well as theoretical, aims to explain how durations are perceived. Although this approach led to important insights, it is fair to say it narrowed the scope of the temporal phenomena researched and explained. Perceived relative timing between events has also been researched, but the theories that try to explain the mechanisms are scarce. An important question that has not been extensively addressed is how we perceive *when* an event occurs, rather than for how long it is present in our environment.

It is well documented in the literature that perceived time depends on the context (Becker & Rasmussen, 2007; Johnston et al., 2006; Karmarkar & Buonomano, 2007a; Miyazaki et al., 2005; Nakajima, Hoopen, et al., 1992; Rose & Summers, 1995; van Rijn & Taatgen, 2008). These findings are important because they provide us with the insights about relevant information for the temporal mechanisms. In the same time, they inform the models of the temporal processing. In particular, the models need to either account for these effects, or explain in a coherent manner why the locus of these effects is not in the temporal processing mechanism. There are still some open questions. For example, it is not clear whether some of the effects are mandatory. Moreover, the research investigating spatial interactions with the perceived time is scarce, compared to that investigating how the temporal context affect the perceived time.

## 1.5 Research Questions in the Thesis

In this chapter I aimed to provide an overview of the relevant work in the time perception that motivated the research presented in this thesis. I presented different conceptualizations of the concept of perceived time, and the effects of context on the perceived duration and relative time between events. Finally, I reviewed the prominent models of the encoding of the different aspects of the temporal information.

The experimental work presented in this thesis is divided in three parts.

In **Part 1** of the thesis I present a project that was motivated by the prominent models of prospective time estimation, that conceptualize timing mechanism as a *clock*. A common attribute of these different dedicated models is a mandatory resetting of the temporal mechanism, at the onset of the event to be timed. However, in the real life, we often do not know in advance that a duration of some event should be estimated. I investigated the accuracy and precision of the perceived duration when no explicit onset of the duration to be estimated was presented. Timing in a more natural context was investigated, and we addressed unpredictability of timed events that, which is an important aspect of estimation in a naturalistic context.

A great part of the introductory chapter was dedicated to the effects of context on perceived duration or relative timing between events. These effects demonstrate that perceived time of visual events is affected by other events presented in their temporal or spatial proximity. In **Part 2** of the thesis I present projects that further addressed this question. In Chapters 4 and 5, I tested whether these effects are mandatory, or they can be reduced or abolished by information about the target identity. In Chapter 6 the effects of spatial location in the visual field on the perceived time of a visual event were tested.

In **Part 3** I present a project that explored the anticipated time of events in the context of an action. In particular, we investigated how the action is timed and self-evaluated as a function of various sources of temporal uncertainty. The question was addressed in two ways. First, a task was designed in a manner that the reaction time and movement duration substantially contributed to the response time. We analyzed how these two components of the action are affected by different conditions in the experiment. Second, participants were asked to self-evaluate their performance, and relation between these judgements and components of the movement were analyzed.



## **Part I**

**The perceived duration with no  
resetting of the clock**



## Chapter 2

# Timing in the absence of a clock reset

As reviewed in the previous chapter, the most prominent models of duration perception propose that in order to encode the elapsed time there is a mandatory resetting of the timing mechanism (Buonomano & Karmarkar, 2002; Ivry, 1996). However, this assumption poses some limitations to the appropriateness of these models for describing time behavior in everyday life. In particular, we often do not know in advance that some event will be important and that its duration should be estimated. We start estimating durations of certain events only after they had started, or even when they are no longer present (retrospective time estimation). Human ability to estimate durations of past events when they were not explicitly timed, is referred to as retrospective timing. In contrast, in prospective timing tasks, time is estimated from the onset to offset of the event, while the event is unfolding in time. In the literature, there is a clear distinction between the prospective and retrospective timing (Fraisse, 1963; Poynter, 1989; Wearden, 2016; Zakay & Block, 2004). However, recent models propose an unified account for the two timing behaviors (French, Addyman, Mareschal, & Thomas, 2014; Shankar & Howard, 2010). In this chapter, I tested the accuracy and precision of perceived durations with a clear, salient onsets compared to the accuracy and precision of perceived durations with implicit onsets. In particular, the notion of timing a visual event without an explicit clock reset is addressed by introducing a novel paradigm that allows us to compare time estimation with and without a cue for resetting the clock.



## 2.1 Abstract

Prominent models of time perception assume a reset of the timing mechanism with an explicit onset of the interval to be timed. Here we investigated the accuracy and precision of temporal estimations when the duration does not have such an explicit onset. Participants were tracking a disc moving on a circular path with varying speeds, and estimated the duration of one full revolution before the stimulus stopped. The onset of that revolution was either cued (explicit), or undetermined until the stimulus stopped (implicit). Reproduced duration was overestimated for short and underestimated for long durations, and variability of the estimates scaled with the duration in both temporal conditions. However, the bias was more pronounced in the implicit condition. In addition, if the stimulus path was partially occluded, duration of the occluded motion was correctly estimated. In a second experiment, we compared the precision in the explicit and implicit conditions by asking participants to discriminate the duration of one revolution before the stimulus stopped to that of a static stimulus presentation in a forced-choice task. Sensitivity of discrimination was worse in the implicit onset condition, but surprisingly, still comparable to the explicit condition. In summary, the estimates follow principles described in prospective timing paradigms, although not knowing beforehand when to start timing decreases sensitivity of temporal estimations. Since in naturalistic contexts, we often do not know in advance which durations might be relevant to estimate, the simple task presented here could become a valuable tool for testing models of temporal estimation.

## 2.2 Introduction

The most influential models of time perception are inspired by a clock metaphor and propose a dedicated clock mechanism to account for human and animal estimation of time (Addyman, French, & Thomas, 2016; Gorea, 2011; Gu, Rijn, & Meck, 2015; Wearden, 2016). One common attribute of different dedicated time models is the notion of mandatory resetting of the clock. For example, in pacemaker-accumulator models, timing of a duration is achieved by accumulating (and counting) events generated by a pacemaker. In order to estimate duration of an interval, a *reset* of the timing mechanism at the onset of the interval is required. This is achieved by opening and closing a switch between the pacemaker and the accumulator (Allan, 1979; Allman, Teki, Griffiths, & Meck, 2014; Gibbon, 1977; Miall, 1989; Treisman, 1963). These models were mostly conceptualized and validated by means of prospective duration estimation tasks. In these tasks, participants

are instructed to begin and end temporal estimation with an onset and offset of the stimulus. This approach had a great success in describing some properties of human and animal temporal estimation, such as the so-called *scalar property of timing* and Vierordt's law. The former property refers to the scaling of the variability of temporal estimates with estimated duration (Allman et al., 2014; Church, 1984; Gibbon, 1977; Lewis & Miall, 2009; Matell, King, & Meck, 2004). Vierordt's law refers to a tendency of temporal estimations to regress to the mean (overestimation of short and underestimation of long durations) (Jazayeri & Shadlen, 2010; Lejeune & Wearden, 2009a; Wearden, 2016), and it has been shown that this regression depends on the uncertainty of temporal estimates (Jazayeri & Shadlen, 2010). In spite of its popularity, the dominant paradigm of prospective duration estimation narrowed the scope of the temporal phenomena being investigated. Importantly, these models cannot explain estimation of time when no clear onset of the duration to be timed is provided. In our daily life, we are sometimes exposed to events that arrive to our senses at unexpected times and that last for variable durations. Since we do not always know beforehand which events could be relevant for us and which durations we would need to estimate, humans must be able to estimate durations of past events even when they were not explicitly timed while unfolding. In the literature, such mechanisms have been referred to as retrospective, in contrast to prospective timing (Fraisse, 1963; Poynter, 1989; Wearden, 2016; Zakay & Block, 2004). The main characteristics of retrospective timing estimation are that one does not know beforehand that duration of a particular interval will be estimated, and so no attention is directed to time while the event is taking place (Block & Gruber, 2014; Grondin, 2010; Wearden, 2016). A timing mechanism that can explain retrospective time estimation has been the focus of recent computational models. These models propose that reconstructing history of neural activation or memory trace are employed for estimation of time (Addyman et al., 2016; French et al., 2014; Shankar & Howard, 2010; Staddon, 2005; Staddon & Higa, 1999). This is a formalization of older ideas about the close relationship between memory about events or changes, and time estimation (Block, 1978; Fraisse, 1963; Liverence & Scholl, 2011; Poynter, 1989). The strength of these models is that they do not need any assumption about an explicit beginning of timing corresponding to the onset of an event. Furthermore, these frameworks unify prospective and retrospective time estimation (Addyman et al., 2016). However, behavioural evidence for timing without clock reset is scarce (Block & Zakay, 2004; Wearden, 2016). In retrospective paradigms participants are asked to estimate the duration of an event only after the event has elapsed. In order not to direct participants to pay attention to passage of time and start timing at the beginning of the event, each participant can be

asked to report duration only once per experiment, which makes these paradigms very costly for the experimenter. Previous studies have shown that retrospective estimates of time tend to be shorter and more variable than prospective estimates, with variability growing faster with duration (Block & Zakay, 1997), although see Boltz (2005). Moreover, despite the fact that models usually explain perceived duration in the milliseconds to seconds range, previous work with retrospective time estimation targeted mostly much longer durations (tens of seconds to minutes) using more cognitive than perceptual tasks and complex stimuli (Grondin, 2010).

In the work reported here, we address the notion of timing a visual event without an explicit clock reset by introducing a novel paradigm that allows us to compare time estimation with and without a cue for *resetting* the clock. We ask participants to estimate the duration of an event linked to a moving stimulus. The stimulus is moving along a circular path with varying speed and the task is to estimate the duration of one full revolution just before the stimulus stopped. We call this revolution, and corresponding duration, *revolution (duration) to be estimated*. In the *explicit onset* condition, the stimulus completes only one revolution, and participants estimate the duration from the beginning to the end of the trial. In the critical *implicit onset* condition, the stimulus moves for a variable duration before stopping. Importantly, in this latter condition, participants do not know when the revolution to be estimated would start. Only when the stimulus stops does the participant know the duration to be estimated. The position where the stimulus stops indicates both where and when the revolution to be estimated started, thus revealing the temporal interval between that position and the moment when the stimulus was on that same position one revolution back. In the *implicit onset* condition, there is no explicit cue for resetting the clock. However, participants were aware that they are estimating the duration on each trial, and inevitably attended to time (Block & Gruber, 2014; Grondin, 2010; Wearden, 2016). Therefore, our task is arguably *prospective* because participants were prepared to estimate time, but also *retrospective* because they needed to go back in time to estimate when an event occurred. Instead of following this terminology found in the literature, we choose a more neutral way to refer to the two tasks (*implicit* and *explicit*). That being said, the task presented here still enables us to address the question of timing when there is no explicit cue to initialise a clock.

## 2.3 Experiment 1A

The purpose of the first experiment was to address two issues. First, we aimed to investigate how well humans can estimate durations in the condition where no

explicit onset of the duration is shown. We compared performance in this novel task to that obtained with a simple prospective duration reproduction task. In order to understand better how the duration of a moving object is computed, we sometimes occluded part of the object trajectory. Humans are very good at extrapolating motion of objects behind occlusions, and at least partly, rely on the same mechanisms as those used when tracking visible motion (Battaglini, Campana, & Casco, 2013; Battaglini & Casco, 2016; Graf, Warren, & Maloney, 2005; Makin, Poliakoff, & El-Deredy, 2009; Olson, Gatenby, Leung, Skudlarski, & Gore, 2004). However, extrapolating occluded motion leads to timing errors, such that the estimated time of an object motion behind occlusions is typically overestimated, and this effect is larger for slower speeds (De Freitas, Myers, & Nobre, 2016; Sokolov & Pavlova, 2003; Yakimoff, Mateeff, Ehrenstein, & Hohnsbein, 1993). In the second part of the experiment we investigated whether temporal errors due to occlusion affect estimated duration of the moving object.

### 2.3.1 Material and methods

#### 2.3.1.1 Stimuli and apparatus

The stimulus was a red disc, size 0.6 deg, rotating along a white circular path, with a radius of 3.7 deg. The background was gray, and the occluder was dark gray. A white fixation dot (size 0.6 deg) was presented at the center of the screen throughout the duration of a trial. In order to make the occluded and not occluded conditions visually similar to each other, an occluder was present in all conditions. In the occluded condition, the occluder was presented on top of the stimulus path, occluding the trajectory of the stimulus (as if the disc was going under a tunnel). In the not-occluded condition, it was presented behind the path and the stimulus moved over it (as if the disc was going over a bridge). The experiment was conducted in a dimly lit room. Experiments were created using Matlab R2016a and Psychtoolbox-3 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) running on a MAC Pro Quadro-Core Intel Xeon with OSX 10.5.8. Stimuli were presented on a LCD flat screen (ViewSonic V3F245), with diagonal 24 in, resolution 1920 x 1080 pixels, and refresh rate 60 Hz. The viewing distance was 50 cm. The analysis of the data was conducted in R Studio environment, using packages “lme4” (Bates, Maechler, Bolker, Walker, et al., 2014) and “lmerTest” (Kuznetsova, Brockhoff, & Christensen, 2017) for mixed effect regression analysis, “Quickpsy” package (Linares, Cos, & Roseboom, 2016) for fitting psychophysics data, and “Bayes Factor” (Morey et al., 2018) for comparing likelihood of regression models.

### 2.3.1.2 Participants

Eight human participants (including two males, overall mean age 23 years) performed Experiment 1. All participants but one (the first author) were naive to the purpose of the study and gave written informed consent and received monetary compensation. The experiment was conducted in agreement with the Declaration of Helsinki and local ethics regulations.

**Procedure** On each trial, participants were tracking the red disc that moved along the circular path. They were asked to reproduce the duration of one full revolution just before it stopped moving (revolution to be estimated) of the disc by pressing a key on a keyboard. The task was to match the temporal interval between the keypress and the disc stop to the interval between the disc stop and the time the disc was at that same position in the previous revolution. A trial started with the presentation of the path for the disc and the fixation point. Participants were instructed to fixate at the fixation point at the centre of the screen. After 200 ms, the disc appeared and started moving in the anti-clockwise direction. The duration of the movement depended on the condition and the interval duration tested. In the *explicit onset* condition, the trial consisted of only one revolution, and participants were instructed to estimate and reproduce how long the disc was moving, from the beginning to the end of the movement. In the *implicit onset* condition, the moving disc made more than one revolution. When the disk stopped, participants were asked to reproduce the duration of the revolution to be estimated, marked by the ending position of the disk (how long it took for the disc to get to this position relative to the previous time it was there). In other words, participants did not know when/where the revolution to be estimated started until the end of the trial. In the experiment, stimuli started moving from the same position but stopped at different positions along the path. The two conditions were tested in separate blocks. We will refer to the two conditions as *explicit onset* if the onset of the duration to be estimated was known, and *implicit onset* if no explicit onset of the duration was presented. A video of a single trial can be downloaded from online version of the article.

Speeds were chosen from the range 0.2 – 1.2 revolutions per second, randomly for each trial. In the revolution to be estimated, the speed was chosen to correspond to one of five interval durations. Durations to be reproduced were logarithmically equally spaced intervals, from 1.1 to 3.5 seconds. We also introduced filler trials, with random durations (5% of trials), in order to make it more difficult for participants to learn and predict durations. In the “implicit onset” condition, the disc moved on average 0.838 seconds (SD = 1.02 sec) before making the revolution to be estimated. The two conditions (*implicit onset* and *explicit onset*) were tested in

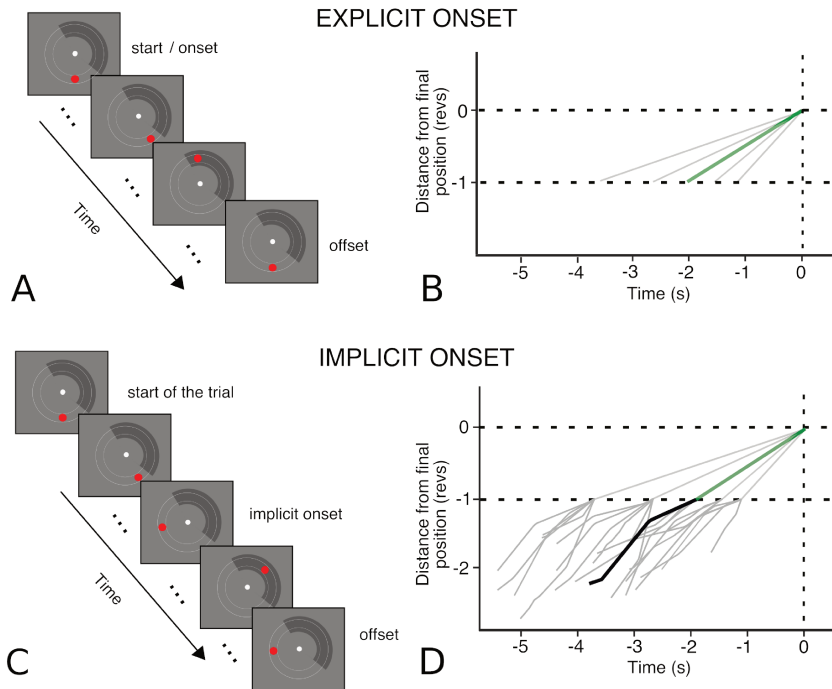


FIGURE 2.1: Illustration of the stimulus sequence in the *explicit* (A and B) and *implicit* (C and D) condition. A. The stimulus started moving in anti-clockwise direction with a constant speed. The stimulus made only one revolution, and participants were asked to reproduce the duration from beginning to the end of the movement. B. Change of the stimulus position as a function of time in the *explicit onset* condition. Lines correspond to five different durations (the middle duration is depicted in green for comparison with the conditions in the *implicit onset* task). In this condition, the stimulus always made only one revolution and started and ended the movement at the same position on the screen. C. In the *implicit onset* condition, the stimulus started moving from the same position as in the *explicit onset* condition (6 o'clock), but since it made more than one revolution its final position was different from trial to trial. Participants did not know where or when the stimulus would stop, so they had to attend to the moving stimulus throughout the trial. When stimulus stopped, they were asked to reproduce the duration of the one-revolution before it stopped. D. The position of the stimulus on the circular path in the *implicit* condition is plotted against the time from the beginning of the trial. Curves illustrate stimulus displacement for the 5 durations. For example, the black-green curve is illustrating one trial where participants were asked to estimate 2 seconds duration. The stimulus started moving with changing speeds for a variable duration (black part of the curve), before making the final revolution (green). When the stimulus stopped, participants estimated the temporal interval of the one-revolution back (temporal interval corresponding to the spatial interval between positions -1 and 0 on the y-axis of the figure). Position and time are aligned with respect to the offset of the disc that defined the duration participants were asked to reproduce. For simplicity only non-occluded trials are shown here (stimulus path was partially occluded in 50% of trials), see Figure 2.2 for occluded conditions.

separate blocks. There were 16 repetitions of each of the durations. Before the beginning of the experiment, there were 30 practice trials with feedback. The experiment lasted about 2.5 hours and participants completed it in two blocks on separate days.

### 2.3.1.3 Occlusion

In order to test whether the reduction of visual information affects the estimation of time, we partially occluded the stimulus path in half of the trials. In the occluded trials, one third of the disc path was occluded with a single occluder and the location of the occluder was varied from trial to trial. The disc never finished its movement behind the occluder. On 12% of the trials, the disc changed its speed behind the occluder, resulting in a conflict with temporal expectation (an example trial is shown in Figure 2.2B). The reason for including these trials was to encourage participants to attend to time rather than position or speed. These few trials were not analysed further.

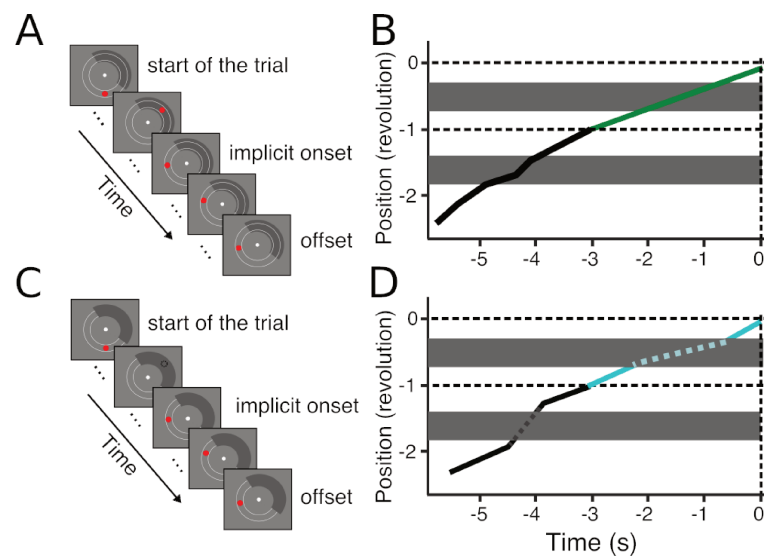


FIGURE 2.2: Illustration of the two trials in the not occluded (A and B) and occluded (C and D) conditions. On panels A and C, stimulus sequence for not occluded (A) and occluded (C) are shown. On panels B and D, not occluded and occluded trials are shown. The duration to be estimated is the same in the two trials, but in the trial shown on panel B, the stimulus is moving at constant speed, and on panel D, it changes speed behind the occluder.

## 2.3.2 Results

### 2.3.2.1 Temporal estimation with and without the explicit onset of duration

In Figure 2.3, reproduced duration is plotted against presented duration for the two temporal conditions, separately for the occluded and not occluded trials. To estimate the accuracy of reproduced durations in the two tasks, for each presented duration, we calculated the reproduction error as the mean difference between reproduced and presented duration.

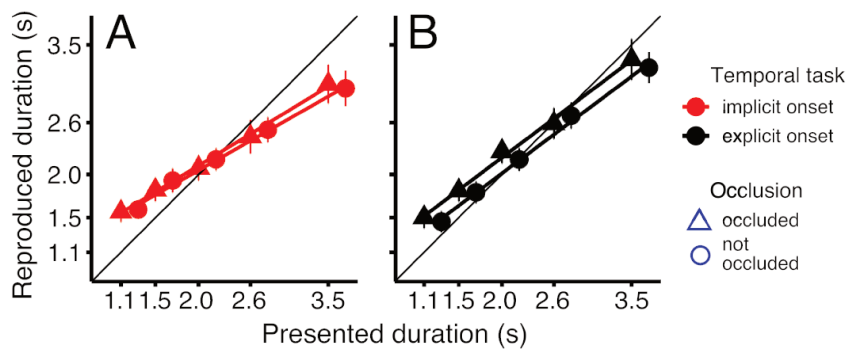


FIGURE 2.3: Reproduced against presented duration for the two temporal tasks (*implicit* in red on panel A and *explicit* in black, panel B). The two occlusion conditions are shown with different marker shapes.

As shown in Figures 2.3 and 2.4, participants were overestimating durations of short intervals and underestimating durations of long intervals. The effect was present in both conditions, but it was smaller for the *explicit onset* condition. We quantified the effect with a linear mixed effect model, using the logarithm of presented duration and temporal task (*explicit onset* or *implicit onset*) as predictors and reproduction errors as the criterion variable. We included participants as a random factor to account for additional variability. We observed the effect of presented duration ( $b = -2.006$ ,  $SE = 0.1$ ,  $t = -18.315$ ,  $p < 0.01$ ), the temporal task ( $b = -0.226$ ,  $SE = 0.053$ ,  $t = -4.240$ ,  $p < 0.01$ ) and their interaction ( $b = 0.823$ ,  $SE = 0.150$ ,  $t = 5.48$ ,  $p < 0.01$ ). Excluding the interaction of the two predictors decreased the goodness-of-fit, quantified by comparing the log-likelihoods of the two models by means of Chi-square analysis ( $\text{Chi-square}(1) = 24.422$ ,  $p < 0.01$ ). This analysis confirmed that the slopes were different from zero, and different between the two temporal conditions (when analysed separately,  $b = -2.010$ ,  $SE = 0.100$  for *explicit* and  $b = -1.16$ ,  $SE = 0.107$  for *implicit onset* conditions).

We assessed the scalar property of time estimation by plotting variability of the estimation (standard deviation) of the reproduced duration as a function of the presented duration (Figure 2.4B). Variability in both conditions scaled linearly with presented duration. To quantify the effect, we conducted a linear mixed model,



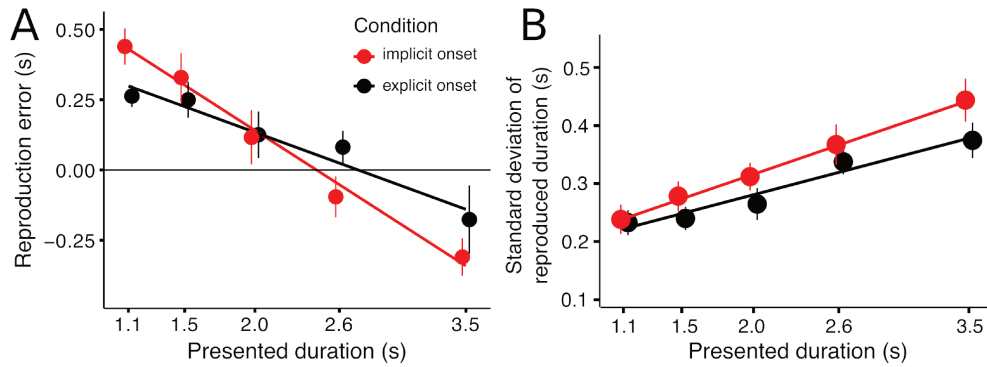


FIGURE 2.4: Bias and variability of temporal estimates in *implicit* (red) and *explicit* (black) onset conditions. A. Mean errors in reproduction averaged across participants are plotted against presented durations. Positive errors indicate overestimation, and negative, underestimation of durations. Participants overestimated short and underestimated long durations. B. Scaling of variability (averaged standard deviation across subjects) of reproduced duration as a function of presented duration. Variability increases linearly with presented duration. Error bars are standard errors of the mean.

with the presented duration and the temporal task as predictors and standard deviation of reproduced duration as the criterion, with subjects as a random factor (intercept only). We observed an effect of presented duration on the standard deviation of reproduced duration ( $b = 0.085$ ,  $SE = 0.01$ ,  $t = 6.198$ ,  $p < 0.01$ ). Even though Figure 2.2B presents a trend for greater variability in the implicit onset condition, coefficients for the temporal condition and interaction were not significantly different from zero ( $b = 0.04$ ,  $SE = 0.045$ ,  $t = 0.099$ ,  $p = 0.921$ , and  $b = -0.02$ ,  $SE = 0.02$ ,  $t = -1.02$ ,  $p = 0.308$ ).

### 2.3.2.2 Temporal estimation is not affected by occlusion

To test whether a reduction of visual information by occlusion affects the estimated duration, we introduced an occluder on the stimulus path on half of the trials. In Figure 2.5, we contrast the errors in the occluded and not-occluded conditions by comparing the mean error per participant for the five presented durations and the two temporal conditions. Reproduction errors were strongly correlated (Spearman's rank correlation  $\rho = 0.835$ ,  $p < 0.01$ ).

To further quantify the effect of the occlusion, we fitted the data with a linear mixed effect model, using temporal errors as the criterion, and the logarithm of presented duration, the two temporal conditions (*explicit onset* and *implicit onset*) and the two occlusion conditions as predictors. The effect of the logarithm of presented duration ( $b = -1.937$ ,  $SE = 0.08$ ,  $t = -23.795$ ,  $p < 0.01$ ), temporal task ( $b = -0.160$ ,  $SE = 0.04$ ,  $t = -4.042$ ,  $p < 0.01$ ) and the interaction of the presented duration with the temporal task ( $b = 0.772$ ,  $SE = 0.114$ ,  $t = 6.719$ ,  $p < 0.01$ ) were significant predictors.

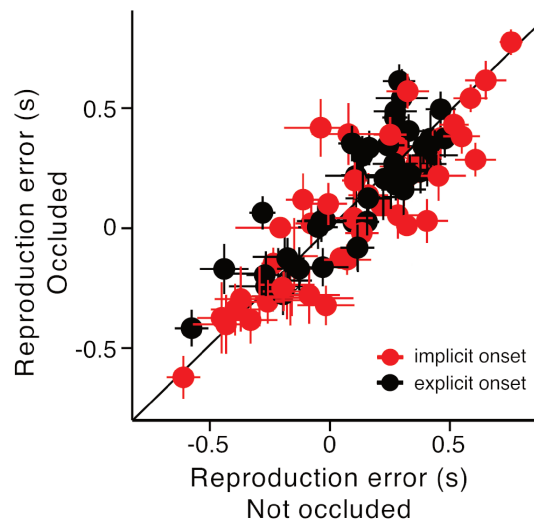


FIGURE 2.5: Reproduction errors in the not occluded, contrasted against errors in the occluded condition. Each symbol is the mean of a different participant in one of the five stimulus durations. Different colours correspond to *implicit* (red) and *explicit onset* (black) conditions. Error bars are standard errors of the mean.

However, there was no effect of occlusion ( $b = -0.01$ ,  $SE = 0.02$ ,  $t = -0.5$ ,  $p = 0.617$ ). We quantified the evidence for no effect of occlusion by means of Bayes Factor (BF). We compared the likelihood of this model with an alternative model that did not include occlusion as a predictor. The Bayes factor reached 19.76, a value considered as strong evidence that performance with and without occlusion were not different (Jarosz & Wiley, 2014; Masson, 2011).

### 2.3.3 Experiment 1B

The aim of Experiment 1B was to address two issues. First, in the main conditions of Experiment 1A, duration to be estimated coincided with a change of speed. Therefore, participants could try to use that information when reproducing durations. In Experiment 1B, speed was not constant in the full revolution just before the stimulus stopped. Additionally, durations to be estimated were not constrained to a set of five values, and instead were in the range from 0.7 to 4.6 seconds (actual values were determined by the number of different speeds and the path length the stimulus was travelling in the full revolution before it stopped). Second, we tested two *implicit onset* conditions. In the first, the speed change coincided with the *implicit onset* of the duration to be estimated, and in the second, the stimulus was moving for more than one full revolution with the same speed before stopping.

#### 2.3.3.1 Material and methods

Stimuli and apparatus were identical to those in Experiment 1A.

### 2.3.3.2 Participants

Eight human participants (two males, mean age 25.4 years) performed Experiment 1B. All participants but the first author were naive to the purpose of the study, signed informed consent and received monetary compensation. The experiment was conducted in agreement with the Declaration of Helsinki and local ethics regulations.

### 2.3.3.3 Procedure

The procedure was similar to the procedure of Experiment 1A. The only difference was that participants completed three separate blocks, two *implicit onset* (speed change or no speed change) and one *explicit onset* (one revolution) conditions. The order of the blocks was counter-balanced across participants. There were 80 repetitions per condition. Before an experimental block, participants performed 30 trials of practice with feedback.

## 2.3.4 Results

To summarize the performance we first binned presented duration in 5 equally sized bins. For each bin and condition we calculated mean reproduced duration, shown on Figure 2.6.

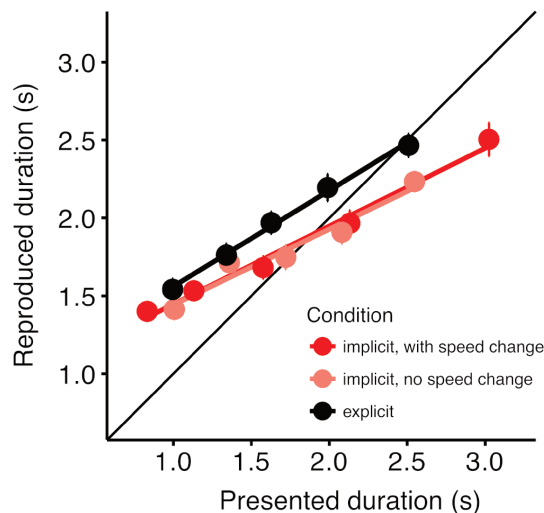


FIGURE 2.6: Bias of temporal estimates in *implicit* (red and light red) and *explicit* (black) onset conditions. Mean reproduced duration in reproduction averaged across participants is plotted against binned presented duration. The three temporal conditions are color coded. Errors bars indicate the standard error of the mean.

As in Experiment 1A, we observed that reproduced durations regressed to the mean presented duration. Also, the effect was larger for the two *implicit onset* conditions. To quantify the effect we performed a linear mixed effect model, with presented duration and the three conditions as predictors, and reproduced duration as criterion variable. We included participants as a random factor to account for variability on individual level.

Not surprisingly, reproduced duration scaled linearly with presented duration ( $b = 0.342$ ,  $SE = 0.021$ ,  $t = 16.08$ ,  $p < 0.01$ ). Importantly, we observed an interaction between presented duration and temporal condition, in the sense that the effect of presented duration was larger for *explicit onset* relative to the *implicit onset* with speed change condition ( $b = 0.120$ ,  $SE = 0.040$ ,  $t = 3.027$ ,  $p < 0.01$ ). Since the presented durations were not constrained, instead of looking at standard deviation of reproduced duration we cannot assess the variability of reproduced duration as in Experiment 1A.

### 2.3.5 Discussion of Experiments 1A and 1B

In the first experiment, we asked participants to reproduce the duration of the full revolution before a stimulus stopped moving along a circular path. The onset of the revolution was not always cued: in an *implicit onset* condition, it was only available to participants retrospectively. We compared performance in this condition to that obtained in a control condition in which the stimulus always made only one revolution. We found that durations were overestimated for short and underestimated for long temporal intervals. In addition, we found a linear relationship between presented durations and variability of reproduction, which is commonly referred to as scalar variability of timing (Allman et al., 2014; Bangert, Reuter-Lorenz, & Seidler, 2011). In the present experiment, the rate at which variability of the estimation increased as a function of presented durations was not different between the two conditions. Finally, there was no effect of the occluder on the performance, and the temporal estimates were unaffected by occlusion of a part of the stimulus trajectory. This finding suggests that even though extrapolation of occluded motion can be biased (De Freitas et al., 2016; Sokolov & Pavlova, 2003; Yakimoff et al., 1993), humans can successfully overcome these biases when estimating the overall duration of an event. We observed an overestimation of short and underestimation of long durations (Figure 2.4A), known as Vierordt's law (Wearden, 2016) or regression to the mean (Allman et al., 2014; Jazayeri & Shadlen, 2010). Even though the effect was shown to depend on the temporal context and uncertainty of temporal estimates (Jazayeri & Shadlen, 2010), we did not observe significant differences in

variability of the temporal estimates. On the other hand, since we used a reproduction task to assess temporal estimates, final variability in estimates included both uncertainties of temporal estimation as well as motor noise. In Experiment 1B, we replicated results from Experiment 1A. We again observed an overestimation of short and underestimation of longer durations for all three conditions, and an interaction of the effect with temporal condition. Additionally, we showed this to be the case even with variable speed in the one-revolution before the end of the motion and for a greater number of durations to be estimated. Finally, whether or not implicit onset coincided with change in speed had no effect on estimated duration. We conducted another experiment to estimate the uncertainty of temporal estimation in the two tasks. In the following experiment, we asked participants to compare the duration of a moving stimulus with that of a static one. By pressing participants to make a forced choice judgment, we eliminated possible biases coming from the reproduction task, and the sensitivity of this paradigm gave us a better estimate of the uncertainty underlying the temporal tasks.

### 2.3.6 Experiment 2

In the first experiment, we showed that humans could estimate the duration of an event even when there was no explicitly cued onset of that event. Estimations in this *implicit onset* condition were nonetheless less accurate than more common prospective ones. In the second experiment, we tested the performance for *explicit onset* and *implicit onset* time estimation in a different task. We presented two stimuli sequentially, a dynamic and a static disc, and participants were asked to compare the durations of the two stimuli. By using binary responses to assess perceived duration, we eliminated possible biases coming from response times and motor noise. Also, information about sensitivity of discrimination in different tasks provided us with additional insight into the way humans estimate time with and without explicitly cued onset of a duration. A final motivation for the present experiment was to test our experimental paradigm in a different task. The dynamic disc was moving on a circular path, as in Experiment 1. It was followed or preceded by the presentation of a static disc, and on each trial participants compared the time it took the moving disc to make one full revolution before it stopped (revolution to be estimated) to the duration that the static disc was presented on the screen. We again contrasted performance in a condition where the dynamic disc made only one revolution (*explicit onset*) with the condition where no explicitly cued onset of the revolution to be estimated was presented (*implicit onset*). Additionally, we introduced another *explicit onset* condition, where the disc made more than one

revolution, but a brief abrupt stopping of the disc cued onset of the revolution to be estimated (in the remainder of the text we will use *one revolution onset* and *cued onset* to differentiate these two conditions). We introduced the cued onset condition in order to check whether exposure to irrelevant motion and varying speeds in the *implicit onset* condition affected temporal estimates and exaggerated differences between the two conditions.

### 2.3.7 Material and methods

Stimuli and apparatus were identical to those in the previous experiment.

#### 2.3.7.1 Participants

Eight participants (including 3 males, overall mean age 25) completed the experiment. One participant failed to understand the task so an additional participant was recruited. The experiment was conducted in agreement with the Declaration of Helsinki and local ethics regulations and all participants gave informed consent.

#### 2.3.7.2 Procedure

We used a one-interval two-alternative forced-choice (1i2AFC) paradigm and asked participants to compare durations of the dynamic disc to that of the static one. On each trial, the dynamic and static discs were presented sequentially (Figure 2.6). The task was to compare the duration of the full revolution before stimulus stopped (revolution to be estimated) of the dynamic disc to the duration of the static disc presentation, by giving a response on the keyboard (choosing between moving or static disc the one that appeared to last longer). The dynamic disc was identical to those in used in Experiment 1, but the duration of the revolution to be estimated was fixed to 1.1 seconds (instead of 5 durations from 1.1 to 3.5 seconds tested in the first experiment). We also decreased the duration of the movement before the revolution to be estimated to an average of 0.4 seconds (standard deviation 0.12 sec), since participants had to sequentially compare the two durations and a long interval between the two would introduce additional memory noise. The static disc was the same red disc, which stayed on the screen for a variable duration. We varied the duration of the static disc in five logarithmically equally spaced steps, from 0.4 to 3 seconds. To mark the offset of both static and moving durations more clearly, stimuli changed their color to blue before disappearing. We used the method of constant stimuli, and the order of presentation was randomized. Each stimulus duration was probed 30 times. The *onset* condition was tested in two blocks, one in which the onset of the targeted revolution was cued by stopping of the stimulus

for 300 ms, and the other where the moving stimulus made only one revolution (Figure 2.7, panels C and D). The total duration of the experiment was 1.5h, with 2 breaks in each block. Before the beginning of the experiment, participants completed 30 practice trials with feedback, but no feedback was provided during the actual experiment.

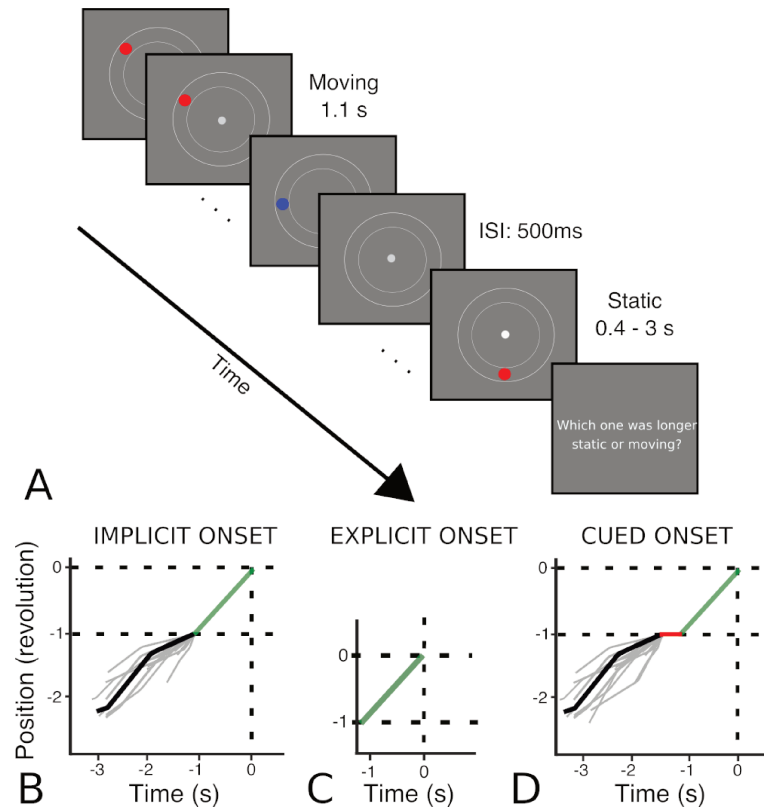


FIGURE 2.7: Illustration of one trial in Experiment 2. A. Participants compared the duration of the targeted revolution of the moving disc with the duration of the static one. B, C and D. Illustrations of trials in the *implicit* and the two *explicit onset* conditions. In the *implicit* onset condition (A), the stimulus moved with different speed for a variable time, before making the targeted revolution. In the *one revolution* onset condition (C), the stimulus made a single revolution. In the *cued onset* condition (D), the stimulus moved for a certain time (black), then stopped for 300 ms to mark the onset (red), and then made the targeted revolution (green).

### 2.3.8 Results

To estimate how well humans can perceive the duration of an event that has no clear onset, we fitted the proportion of responses the static stimulus was judged to be longer as a function of the static stimulus duration with a cumulative normal distribution (Figure 2.8A). For each participant and condition (*implicit onset* and two *explicit onset* conditions), we calculated the point of subjective equality (PSE)

and the discrimination sensitivity. The PSE was the duration that led to 50% probability of judgments either *shorter* or *longer* than the standard, and the sensitivity was taken to be the inverse of the standard deviation of the fitted normal distribution. Sensitivity of the duration discrimination between the static and the moving stimuli is shown on Figure 2.8B. There was a trend of a decrease in sensitivity, where the condition with one revolution having the largest and the *implicit onset* condition the smallest sensitivity. To compare sensitivities in the three conditions, we conducted permutation tests for each condition against the other two conditions (3 comparisons in total). We permuted the data from a pair of conditions for each participant 10,000 times and analysed the distribution of differences in two sensitivities, randomly assigned to one of the two conditions. We analysed the data of seven participants, excluding one participant whose sensitivity in the *one revolution onset* condition was outside the 1.5 interquartile range. Permutation tests showed that sensitivity was indeed significantly larger in the *one revolution onset* compared to the *implicit onset* condition ( $p = 0.02$ ), but the other two comparisons were not significantly different from the distribution of random variations (two *explicit onset* conditions:  $p = 0.1$  and *implicit onset* and *cued onset*  $p = 0.096$ ).

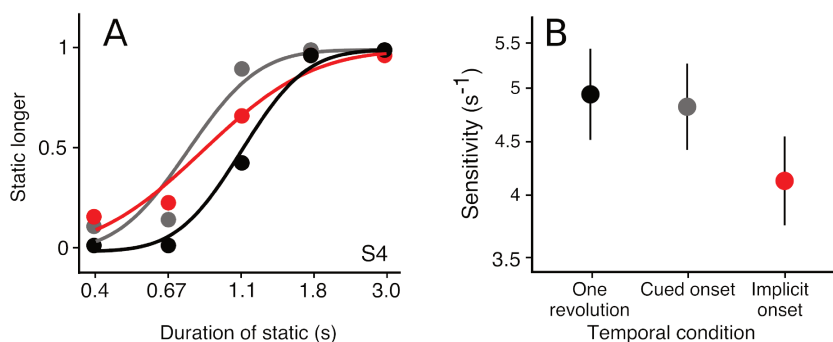


FIGURE 2.8: Performance in Experiment 2. A. Psychometric function of one participant. The proportion of judgments *static longer* is plotted against duration of the static stimulus on a logarithmic scale. B. Sensitivities (inverse of slopes of the curves on panel A) for the three conditions averaged across participants. Error bars are standard errors of the mean.

We observed considerable variability in the perceived duration of the moving stimulus for the *implicit onset* and the *cued onset* condition. The three permutation tests showed that the actual observed differences in each pair were not different from random differences obtained by permutations (the probability that observed differences were due to random variations was 0.71 for the difference between two *explicit onset* conditions, 0.755 for *one revolution onset* and *implicit onset*, and 0.794 for the *cued onset* and *implicit onset* conditions).



To investigate whether the order of stimuli presentation affected performance, we analysed the data separately for the two ordering presentations (static stimulus presented first or second). As shown in Figure 2.9, performance was better if the static stimulus was presented after the moving one. This was true for the *implicit onset* (permutation test for the difference,  $p = 0.007$ ) and *cued onset* conditions ( $p = 0.008$ ), but it did not reach significance for the *one revolution onset* condition (0.087).

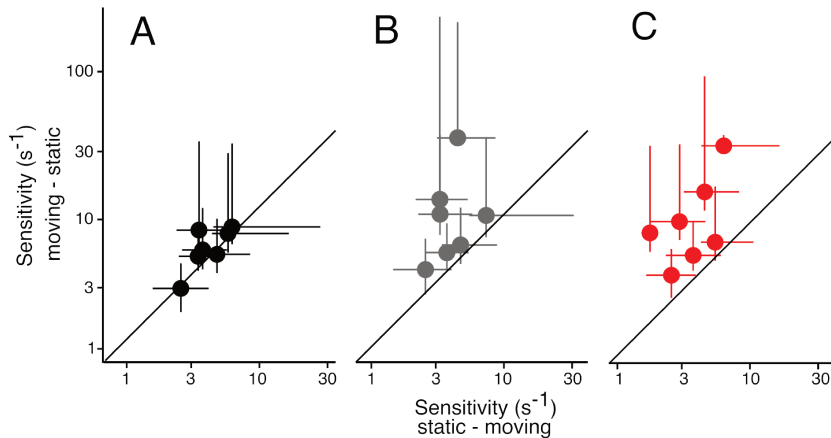


FIGURE 2.9: Effect of the order of presentation on sensitivity. Sensitivities (inverse of the standard deviation of fitted psychometric function on a logarithmic scale) for the two orders of presentation are plotted against each other. Each symbol represents one participant in one of the three onset conditions. A. One revolution onset condition. B. Cued onset condition. C. Implicit onset condition. Data for one participant were omitted in the two “explicit onset” onset conditions (B and C) because it was not possible to obtain reasonable fits with fewer points per stimulus level.

### 2.3.9 Discussion

In the second experiment, we asked participants to compare the duration of one revolution before the stimulus stopped moving (revolution to be estimated) of a dynamic disc to that of a static disc. We compared performance across three conditions, two *explicit onset* (*one revolution onset* and *cued onset*) conditions and one *implicit onset* condition. We found no systematic biases in perceived duration for the three conditions. However, sensitivity were greater in the *one revolution onset* condition, indicating that participants could discriminate durations better when the onset of the duration to be estimated was known. Interestingly, the condition in which the onset of the revolution to be estimated was cued by a brief stopping of the stimulus was not better than the implicit onset condition and not worse than the one revolution onset, indicating that introducing a an explicit cue is not sufficient to completely isolate a temporal event. To investigate whether working memory load affected performance in our task, we analyzed the trials separately depending

on the order of presentation (whether the static disc was presented first or second). If maintaining a representation of duration indeed affected performance in our task, we would expect that sensitivity would depend on the order of presentation. In the trials in which the static disc was presented first, participants had to maintain the duration of the static disc for longer, as these trials included irrelevant motion at the beginning of the second disc that was in motion. We would therefore expect performance to be worse in these trials. The analysis of our results showed that there was indeed a cost in sensitivity when there was irrelevant motion at the beginning of the second disc. Interestingly, this cost disappeared in the *one revolution onset* condition where both discs were only presented for the duration to estimate. These results are in agreement with previous findings showing that non-temporal task demands interfere with time estimation, in both prospective and retrospective tasks (Brown, 1985; P. Brown, Rothwell, & Marsden, 1997; Üstün, Kale, & Çiçek, 2017). Furthermore, it has been shown recently that discrimination of two stimuli is affected by their order and recent history (Nachmias, 2006; Raviv, Ahissar, & Loewenstein, 2012; Raviv, Lieder, Loewenstein, & Ahissar, 2014). More specifically, the representation of the first stimulus in a trial with two sequentially presented stimuli is affected by past stimuli, and the decision is based on a comparison between the corrupted first and the uncorrupted second stimulus. Extending this finding to our results, we could assume that the noisier the representation, the greater the influence of recent history. Given that the three temporal conditions differ in the amount of uncertainty, the influence of the previous stimuli (which in our experiment converge to the value of the reference), would decrease the difference between the test and the standard to different extents depending on the condition.

## 2.4 General Discussion

In the present study, we investigated the accuracy and precision of temporal judgments when the duration to be estimated does not always have an explicit onset. We designed a novel task and compared performance in this task to that in the classic prospective time estimation paradigm in two separate experiments. We asked participants to track a disc moving on a circular path with varying speeds. When the stimulus stopped, participants had to estimate the duration of the full revolution before the disc stopped moving. We manipulated the explicitness of the onset of the temporal interval in three conditions. The onset was either retrospectively revealed to participants (*implicit onset*, Experiments 1 and 2), or it was known

beforehand since the stimulus made only one revolution (*one revolution onset*, Experiments 1 and 2), or it was cued by an abrupt brief stopping of the disc (*cued onset*, Experiment 2). We assessed temporal estimation in two different tasks, either by asking participants to reproduce perceived duration or to compare it to the duration of a static disc. In both the *explicit onset* and *implicit onset* conditions, we found two classical signatures of time estimation: regression to the mean and scaling of the variability with the estimated duration. These findings are in agreement with previous studies showing similarities between prospective and retrospective timing estimation (Boltz, 2005) and models that assume the same mechanisms for timing in both contexts (French et al., 2014; Shankar & Howard, 2010). The main difference between the two temporal conditions was the size of the effects. More specifically, we found that the regression to the mean, also known as Vierordt's law, was larger in the *implicit onset* condition than in the *explicit onset* condition. Since it has been proposed that Vierordt's law is related to the uncertainty of temporal estimates, the difference between the two conditions could come from differences in the variability of the temporal estimates (Jazayeri & Shadlen, 2010). In line with this hypothesis, in Experiment 2 we found that sensitivity of temporal discrimination was indeed larger in the *one revolution onset* relative to *implicit onset* condition. In all conditions of the two experiments, participants were aware that their task was to estimate the duration of the moving stimulus. Therefore, they were always attending to time. We designed the *implicit onset* experiment in a way to prevent some strategies, such as estimating time from speed (speed changes multiple times within a trial), using landmarks (random stopping position across trials) or counting. In addition, in Experiment 1B, we showed that trials in which stimulus speed changed at the onset of the target were not different from trials in which there was no change of speed (the stimulus was moving with a constant speed for more than one revolution before stopping), suggesting that participants were not using speed changes as a cue. In a control experiment, we found that participants were not able to reliably detect the onset of the targeted revolution even when they were explicitly asked to do so. We asked 5 participants who had previously completed the duration reproduction experiment to press a key on a keyboard as soon as they believed that the targeted revolution had started. None of the participants were able to reliably identify the target (hit rates within 20 to 40%). Details of this experiment are shown in Appendix. Can we assume that the same mechanism is underlying the performance across the two temporal conditions in spite of differences in variability of estimates? From previous work on visual working memory, we know that prioritization of an item leads to its enhanced recall (Gorgoraptis, Catalao, Bays, & Husain, 2011). Since in the *explicit onset* conditions the beginning of the revolution

to be estimated is explicitly cued, we could assume that it has been memorized with greater precision. Therefore, the same mechanism in both tasks could be underlying temporal estimation (e.g. sampling of decaying activation trace (French et al., 2014) or reconstruction from temporal context vectors (Shankar & Howard, 2010), while the difference in variability originated from the precision in memorizing the onset of the revolution. In the second experiment, sensitivity of temporal judgements was affected by the order in which stimuli were presented. In particular, temporal judgements were worse in *implicit* and *cued onset* conditions if the static stimulus was presented first. This finding suggests that working memory load, present in both *implicit onset* and *cued onset* conditions, affects our ability to compare temporal intervals. The difference in sensitivity could be explained by the effect that past history has on the representation of the first stimulus in the sequence (Raviv et al., 2012, 2014). It is an open question, however, whether the effect of memory load on temporal estimation also indicates a close relationship, and possibly a shared neural mechanism between working memory and time estimation, as suggested by previous work (P. Brown et al., 1997; Gu et al., 2015; Muller & Nobre, 2014). To better understand the mechanisms underlying time estimation in our task, it will be pertinent to investigate the parameters affecting performance in explicit and implicit onset conditions. For example, cognitive load has different effects on prospective and retrospective time estimation (Zakay & Block, 2004). Introducing a concurrent task should help us determine if the temporal estimations under uncertainty about the onset of an event require different mechanisms than timing from the beginning to the end of an interval.

## 2.5 Supplementary experiment

A reasonable doubt is whether participants can detect that the final revolution started before the end of the trial. However, here we aimed to investigate how well humans can estimate duration when interval does not have a clear onset. Even if participants can suspect that the stimulus will stop moving in near future, we are still addressing the question of interested, although our inference is less clear. If participants suspect that stimulus will soon stop, even if they start timing prospectively from that moment, they still have to estimate the fraction of the duration between the moment they decided it was the last revolution and the estimated onset of the last revolution. To more closely address this question, we looked into distribution of mean path length in degrees) that stimulus was making in one trial before making the last revolution. Median of the distribution (shown in magenta on S1.1) is 105 degrees (median absolute deviation = 60 deg), suggesting that once the stimulus was moving with the same speed for longer than one third of the path, participants could suspect that it stimulus was going to stop in less than one revolution.

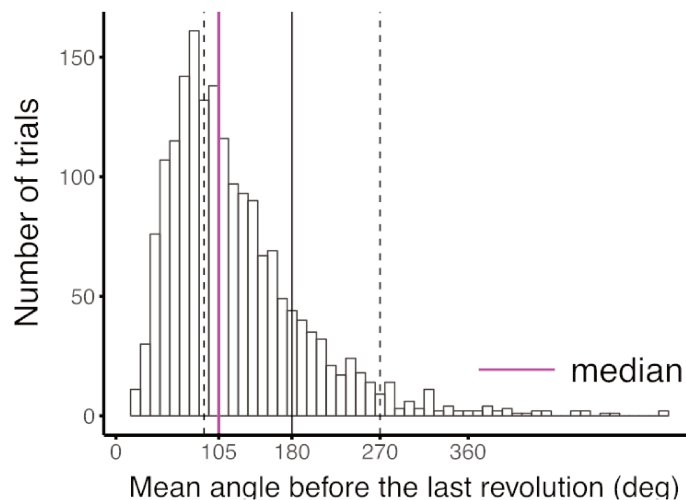


FIGURE 2.10: Distribution of mean path (deg) stimulus was moving with different speed before *implicit* onset. Data from all participants are plotted here. Median is shown in magenta.

We investigated whether participants could detect the onset of the -1 revolution when they are explicitly asked to do so. We asked 5 participants who have previously completed duration reproduction experiment to press a keyboard key as soon as they believe that the last revolution is being presented. The stimuli they saw were trials with the 5 durations from the first experiment (only 5 durations i.e. 5 speeds, no trials where speed was changing). On panel A of Figure 2.11 proportion of correct answers is plotted for each subject. None of the subjects was able

to reliably identify the target. In an informal debriefing after the experiment, participants reported that even though they detected that stimulus was moving with constant speed for certain time they were not confident that it's indeed the target, since the stimulus would also sometimes change speed after moving with a constant speed for longer time. On panel B of the Figure 2.11 distribution of stimulus positions at the moment of key press is plotted for a single subject.

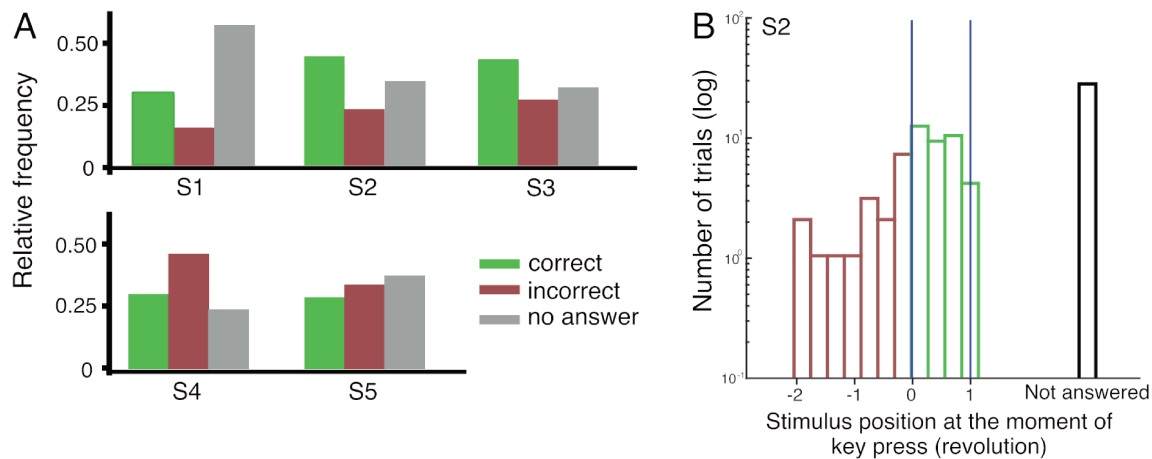


FIGURE 2.11: Proportion of correct detection of the final revolution. On panel A proportion of the correct, incorrect answers and trials in which stimulus stopped moving before participants gave an answers. Participants were correct in 20-40% of the trials. On panel B shows distribution of stimulus positions (relative to the *implicit onset*). Trials in which participant pressed the key after the *implicit onset* are shown in green, and those in which key was pressed too early in red. Trials in which no response was given before the stimulus stopped are shown in black.

## 2.6 Conclusions

In the present study, we investigated the accuracy and precision of temporal judgments of durations with onsets that were revealed retrospectively. The accuracy and precision of perceived durations were tested in two conditions: durations with a clear, salient onsets, and durations with implicit onsets, that was revealed retrospectively. We found that the temporal context affected the estimates more in the *implicit* onset condition, and the estimates were more biased towards the mean of the presented durations. In addition, the temporal discrimination sensitivity was larger in the *explicit* relative to the *implicit onset* condition.

We designed a novel task to address how explicitness of the duration onset affects the perceived duration. One of the limitations of the task we have introduced here is the link between stimulus speed and interval duration. To completely break this relationship, the stimulus would need to travel at non-constant speeds over parts of the trajectory, for instance, by smoothly accelerating and decelerating throughout the stimulus presentation. Another limitation is that very short durations cannot be tested, although presumably one could reduce the radius of the stimulus path. From the experiments described here, as well as other piloting work, we believe that the present paradigm is best suited for testing temporal estimation of durations in the 1 to 10 seconds range.

In the work presented here, we investigated timing in a more natural context, since in real life, we often do not know in advance that a relevant event is about to start. As in our experiment, it is often the case that only when an event is finished do we need to estimate when it started or how long it lasted. Even though our stimuli and tasks are still far from an actual naturalistic context, we believe that they do address one of the key aspects of naturalistic time estimation: the unpredictability of events to be timed.

## **Part II**

**The perceived time of events depends  
on their temporal and spatial context**





In Part 2 of the thesis, I investigated how the perceived time of visual and auditory events is affected by their temporal and spatial context. As presented in the introductory chapter, the perceived time of events is greatly dependent on the context (Karmarkar & Buonomano, 2007b; Nakajima, Hoopen, et al., 1992; Rose & Summers, 1995; Suetomi & Nakajima, 1998). Here I investigated to what extent the effects of the context are mandatory. In particular, is the perceived time of a visual target different depending on how we attend to it, or on its temporal context? In Chapter 3 the perceived time of the visual stimulus was investigated in the temporal context of other visual events. In Chapter 4, I investigated interactions between the perceived time of the auditory and visual stimuli. Work presented in Chapter 5 explored perceived time across the visual field.

Before proceeding to the chapters, I will briefly discuss the task used in experiments in this chapter. The differences between relative and absolute perceived position are well acknowledged in studies of spatial localization, for both the visual (Klein & Levi, 1987; Westheimer, 1975) and auditory (Recanzone, Makhamra, & Guard, 1998) modality. For example, relative visual acuity thresholds are an order of magnitude greater than absolute ones (Westheimer, 1975). Most measures used in studies of the perception of duration and succession cannot answer the question of when a single event is perceived. That said, due to the sequential nature of time perception, to be able to estimate when an event happened, we need to relate it to some reference (before or after X), and estimate how much time elapsed from that reference. In Chapters 4 and 6 I investigated when an event is perceived, relative to the fixed duration of a trial duration. The procedure used by Libet et al. (1983) was adapted to investigate the perceived time of visual events. A similar method has recently been adapted to study the duration of the spatial attention shifts (Carlson, Hogendoorn, & Verstraten, 2006), and the timing of multisensory events (Fendrich & Corballis, 2001).



## Chapter 3

# When an event is perceived depends on how we attend to its temporal context

Great body of work investigating perceived spatial position showed that stimuli presented in spatial and temporal proximity of the target stimuli affect its perceived position (Chien, Ono, & Watanabe, 2011; Chow, Gozli, & Pratt, 2014; Liverence & Scholl, 2011; Ono & Watanabe, 2011; Suzuki & Cavanagh, 1997). How the perceived time of events is affected by other events in their temporal proximity has been far less researched (Burr et al., 2013; Karmarkar & Buonomano, 2007a; Nakajima, Ten Hoopen, Hilkhuisen, & Sasaki, 1992). In the work presented in this chapter, I investigated how events presented in the temporal proximity of the target affect its perceived time. In addition, I tested whether the knowledge of the target order or color modulates the effect of the distractor.

### 3.1 Abstract

We investigated whether the moment when an event is perceived depends on its temporal context. Participants learned a mapping between time and space by watching the hand of a clock rotating a full revolution in a fixed duration. Then, the hand was removed, and a target disc was flashed within this interval duration. Participants had to indicate where the hand would have been at the time the target was flashed. In three separate experiments, we estimated the disruption of another distractor disc that was presented before or after the target, with variable time between them. The target was either revealed at the end of the trial, or cued beforehand, and in this latter case, either by its color or temporal order. We found an attraction to the presented time of the distractor when both events were equally attended (target revealed at the end). When the target was cued beforehand, the reported time was under or overestimated, depending on whether the nature of distractor had to be decoded (*pre-cued by color*) or not (*pre-cued by order*). These results illustrate the variety of ways the time of an event can be altered by other nearby events and by what we attend to.

### 3.2 Introduction

Perception of time is malleable. For example, the perceived duration between two attended events is affected by irrelevant *distractor* events presented before or after them (Burr et al., 2013; Karmarkar & Buonomano, 2007a; Nakajima, Ten Hoopen, et al., 1992). The longer the duration between the distractor and the first event, the stronger the bias to perceive the duration between the two attended events as longer. The attraction towards the duration of the distractor interval is explained by a tendency to regularize the sequence of the three events constituting the intervals (Burr et al., 2013; Remijn et al., 1999; Sawai et al., 2012). Although implicit in the regularization hypothesis, we do not know whether perceived time of a single event is affected by the context. Here, we are asking whether the moment when an event is perceived is affected by other events presented in its temporal proximity. As we investigate how the perceived time of an event is influenced by its context, it is informative to recall how the perceived spatial position of visual events is also affected by other events in their spatial and/or temporal proximity. For example, perceived spatial position of a target can be either attracted or repelled from a distractor, depending on the temporal order between the two (Chien et al., 2011; Chow et al., 2014; Ono & Watanabe, 2011; Suzuki & Cavanagh, 1997). In the multiple object spatial tracking task, perceived space can be either compressed or

expanded, depending on whether the events are attended to or not (Liverence & Scholl, 2011). We aim to extend these findings to the moment when an event is perceived. In three different experiments, we varied when and how the target was cued. The target was revealed only at the end of the trial (*post-cued by color*), or cued beforehand by its color (*pre-cued by color*), or temporal order (*pre-cued by order*).

## 3.3 Methods

### 3.3.1 Stimuli

Stimuli were red and green discs of radius 1 degree of visual angle (dva), briefly flashed (33 ms). Fixation was a 0.5 dva white disc that changed its luminance to dark gray as a preparation signal, just before the beginning of the trial. At the beginning of the trial, fixation changed into a place-holder for the stimulus, a white circle, that had same size as stimuli. During the experiment, a white circle, representing the face of the clock was always present. The hand of the clock was shown only during the familiarization phase. The face and the hand of the clock had radius of 2.5 dva and the same white color. Each trial started and ended with a 33 ms pure tone of frequency 1kHz. Apparatus The experiment was conducted in a dimly lit room. Experiments were created using Matlab R 2016a and Psychtoolbox-3 (Brainard, 1997) running on a MAC Pro Quadro-Core Intel Xeon with OSX 10.5.8. Stimuli were presented on a LCD flat screen (ViewSonic V3F245), with diagonal 24 in, resolution 1920 x 1080 pixels, and refresh rate 60 Hz. The viewing distance was 50 cm. The analysis of the data was conducted in R Studio environment, using the “lme4” package (Bates et al., 2018) for mixed-effects regression analysis. We excluded trials with errors larger than 120 degrees from analyses (less than 5% of the trials were excluded).

### 3.3.2 Participants

Twenty-four participants took part in the experiments (including 6 males, overall mean age 24.6 years). All but one participant (the first author, who participated in the *post-cued by color* experiment) were naive to the purpose of the study and gave written informed consent. We tested eight participants in each experiment, and this sample size was chosen based on similar previous studies (Libet et al., 1983). The experiment was conducted in agreement with the Declaration of Helsinki and local ethics regulations.

### 3.3.3 Procedure

At the beginning of the experiment, participants were familiarized with a fixed trial duration, by watching the hand of a clock rotating at a constant speed, one cycle in 2 seconds. To provide additional cues, and to facilitate learning of the trial duration, a brief tone (33 ms, 1kHz) was presented at the beginning and the end of each revolution. In the rest of the experiment, the hand was not presented. The clock face was represented during the trial as a circle, and the two tones were presented at the beginning and the end of each trial. Participants were asked to fixate the fixation circle presented at the center of the clock face. After a variable duration from the beginning of the trial, two stimuli were briefly presented in temporal sequence. Participants were asked to attend to the time from the beginning of the trial, and to estimate when the stimuli were briefly presented, relative to the beginning and the end of the trial. They gave their response at the end of the trial by placing a cursor on the face of the clock at the location where the hand of the clock would have been at the time of the stimulus. Participants always reported when one of the two stimuli were presented. We will refer to the stimulus that they were asked to report as the target, and the other stimulus of the pair as the distractor. On each trial, the presented time of the target within the trial interval was chosen randomly. The time of the distractor relative to the target was chosen following the method of constant stimuli, and could take one of 10 levels, from  $-300$  ms (the distractor before the target) to  $+300$  ms (the distractor after the target). In the *pre-cued by color* and *post-cued by color* experiments, we also presented trials in which only one stimulus was presented (9% of trials). We never presented a stimulus (target or distractor) within 150 ms after the beginning or before the end of the trial.

In three experiments, we varied how and when the target was revealed. In the *post-cued by color* experiment, participants were asked to attend to both events, and only at the end of the trial, the target was revealed by its color. In the other two experiments, participants knew in advance which event they would be asked to report, and the target was cued either by color (*pre-cued by color*) or temporal order (*pre-cued by order*). In the *post-cued by color* and *pre-cued by order* experiments, the two colors were randomly assigned to the two stimuli on each trial.

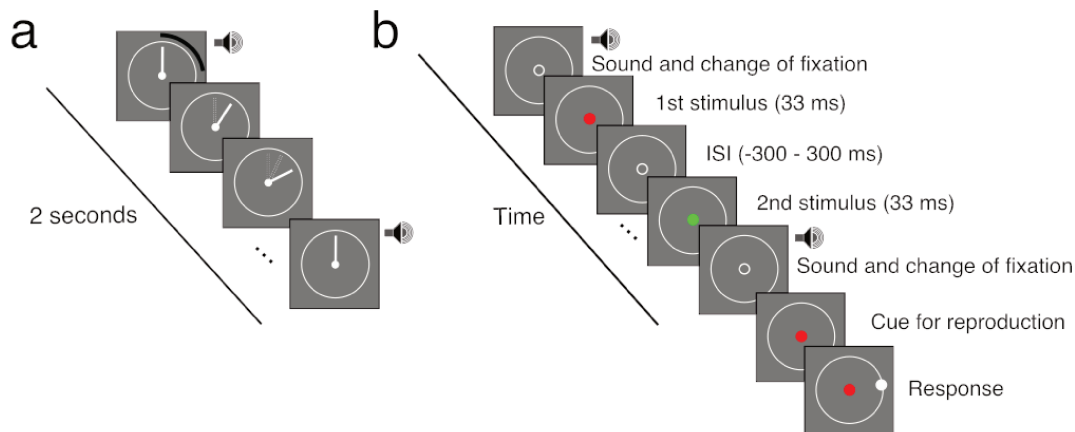


FIGURE 3.1: Chronology of the familiarization phase and of an experimental trial. (A). Familiarization with trial duration. Participants were presented with a clock at the beginning of the experiment and after each break. The hand of the clock rotated at a constant velocity over 2 seconds for one full revolution. A brief 1kHz pure tone was presented at the beginning and at the end of each revolution, as an additional cue to facilitate learning of the trial duration. (A). Illustration of the chronology of the *post-cued by color* experiment. During the experiment, the hand of the clock was removed but the white circle representing the face of the clock remained on the screen. At the start of the trial, the fixation disc changed to a placeholder for the stimulus, and a brief tone was presented. After a random delay, two stimuli were successively presented, one red one green, in random order. The trial lasted 2 seconds, and the end of the trial was marked by a change of the placeholder to a fixation disc and a brief tone. When the trial ended, one of the two discs was presented again to indicate the color of the target disc. Participants moved the mouse cursor to place it on the clock face at the location where the hand of the clock would have been at the time of the target presentation. The procedure was similar in the *pre-cued* experiments, except that participants knew beforehand the color (red/green) or the temporal order (first/second) of the target and the distractor. In *pre-cued experiments*, the two colors and temporal orders were tested in separate blocks.

## 3.4 Results

### 3.4.1 When an event is perceived is affected by other events presented before or after it

To estimate the accuracy of the perceived time of the target, we calculated the temporal error as a difference between reported and presented times. In Figure 3.2, the average error across participants in the *post-cued by color* experiment is plotted against different temporal delays between distractor and target.

In the *post-cued by color* experiment, the reported target time was attracted to the presented time of the distractor (Figure 3.2). The moment when the target was perceived was reported later if the distractor was presented after the target. We quantified the effect by means of a linear mixed-effects model, where we modeled



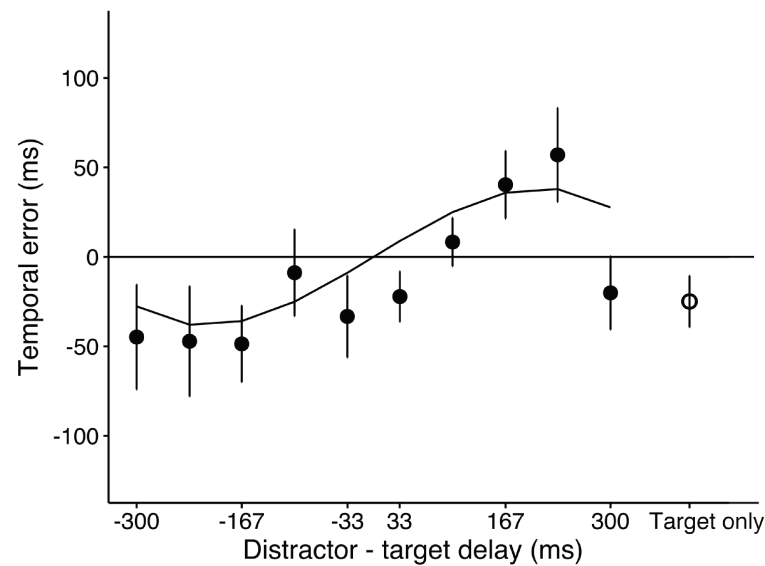


FIGURE 3.2: Attraction to the timing of the distractor in the *post-cued by color* experiment. Average temporal error across participants is plotted against different temporal delays between distractor and target. The reported time of the target was biased to the moment when the distractor was presented. The target was reported later (positive temporal error) if the distractor was presented after, and reversely when it was presented before. Temporal error in condition where only one stimulus was presented is shown in open symbol. Black line is the result of a linear mixed-effect model fitted to the data. Error bars correspond to standard error of the mean (Loftus & Masson, 1994).

the fixed effect of the delay between the target and the distractor as a third order polynomial. We included subjects as a random factor (intercept) to account for additional variability. We observed a significant effect of the delay between the target and the distractor; estimates of when the stimulus was presented were biased towards the timing of the distractor ( $b = 0.264$ ,  $SE = 0.065$ ,  $t = 3.998$ ,  $p < 0.01$ ). Also, the cubic term of the polynomial was significant ( $b = -1.972$ ,  $SE = 0.936$ ,  $t = -2.106$ ,  $p < 0.05$ ), indicating that the effect of the distractor decreased with increased temporal distance between the target and the distractor (when the distractor was sufficiently remote from the target, its attraction vanished). Excluding the cubic term significantly decreased the goodness-of-fit of the model, as assessed by a comparison of the models log-likelihoods with a Chi-square test ( $\text{Chi-square}(1) = 4.413$ ,  $p < 0.05$ ).

We conducted the same analysis for the other two experiments. In *pre-cued by color* experiment, we found a significant intercept ( $b = -0.064$ ,  $SE = 0.019$ ,  $t = -3.307$ ,  $p < 0.01$ ), accounting for the large negative bias (pink symbols in Figure 3.2B). However, none of the polynomial terms were significant ( $b = 0.110$ ,  $SE = 0.064$ ,  $t = 1.706$ ;  $b = 0.154$ ,  $SE = 0.148$ ,  $t = 1.040$ ;  $b = -0.736$ ,  $SE = 0.917$ ,  $t = -0.824$ ). In *pre-cued by order* experiment, we found a significant effect of the distractor; the reported

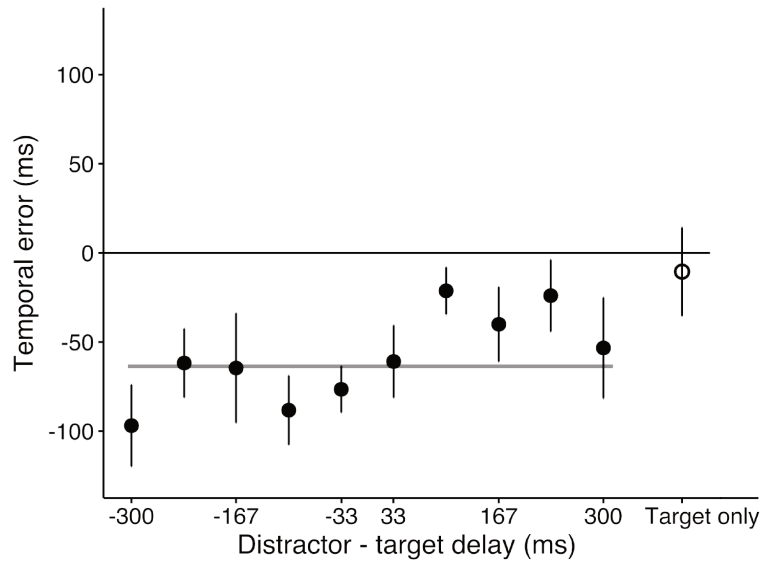


FIGURE 3.3: Bias in reported time of the target in the *pre-cued by color* experiment. Average temporal error across participants is plotted against different temporal delays between distractor and target. The target was overall reported earlier. Temporal error in condition where only one stimulus was presented is shown in open symbol. Error bars correspond to standard error of the mean.

time of the stimulus was biased away from the presented time of the distractor ( $b = -0.176$ ,  $SE = 0.06$ ,  $t = -2.911$ ,  $p < 0.01$ ). Again, the cubic term of the polynomial was significant ( $b = 2.093$ ,  $SE = 0.856$ ,  $t = 2.444$ ,  $p < 0.05$ ), indicating that the effect of the distractor decreased with increasing temporal distance between the target and the distractor. Excluding the cubic term significantly decreased goodness-of-fit (Chi-square(1) = 5.9731,  $p < 0.05$ ).

To confirm that our results can be generalized to trials that have durations other than 2 seconds, we conducted an additional experiment. Procedure, stimuli and distractor conditions were the same as in *post-cued by color* experiment, and the only difference was that the duration of the trial was now fixed to 1.5 seconds. We recruited eight new participants for this experiment. As in the previous experiment, we analyzed the data with a mixed-effects model, with difference in timing between target and distractor as a predictor and temporal error as the dependent variable. We modeled the effect of the distractor as a third order polynomial (3 predictors, delay, delay2 and delay3) to describe the non-linearity of the effect. Finally, we included participant as a random factor. We observed a significant positive effect of the distractor ( $b = 0.116$ ,  $SE = 0.048$ ,  $t = 2.411$ ,  $p < 0.05$ ). The second and third order terms were however not significant ( $b = -0.0935$ ,  $SE = 0.112$ ,  $t = -0.835$ ,  $p = 0.404$  and  $b = -0.911$ ,  $SE = 0.688$ ,  $t = -1.324$ ,  $p = 0.186$ , respectively).

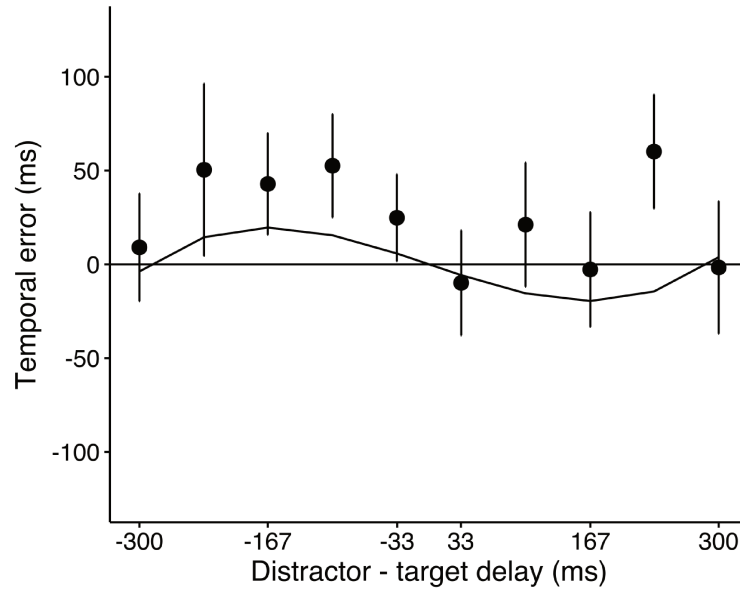


FIGURE 3.4: Bias in reported time of the target in the *pre-cued by order* experiment. Average temporal error across participants is plotted against different temporal delays between distractor and target. The reported time was repelled from the time of the distractor. The repulsion effect was more pronounced for trials where distractor was presented before the target. Error bars correspond to standard error of the mean.

### 3.4.2 When an event is perceived depends on how we attend to events in its temporal proximity

Temporal errors for each cueing experiments and temporal order between target and distractor are summarized in Figure 3.2B. Additionally, the average temporal errors for the conditions in which only the target was presented (no distractor) are shown. As it can be seen in Figure 3.2B, different cueing methods create different biases. In the *post-cued by color* experiment, the target was on average reported later (positive temporal error) if the distractor was presented after it. When the target was pre-cued by color, targets were reported earlier than presented. In *pre-cued by order* experiment, the target was reported later if the distractor was presented before it. To compare the bias in the three experiments, we fitted the data with a linear mixed-effects model. The dependent variable was the temporal error, and the predictors were the temporal delay between the target and the distractor, and the experiment. We also tested interactions between the predictors, and included participants as a random intercept, to account for the additional variability. Only trials in which the distractor was presented were included in the model. The effect of the temporal relation between the target and the distractor was positive, indicating that the temporal error was more positive when the distractor was presented after the target ( $b = 0.1356$ ,  $SE = 0.0258$ ,  $t = 5.254$ ,  $p < 0.01$ ). Furthermore,

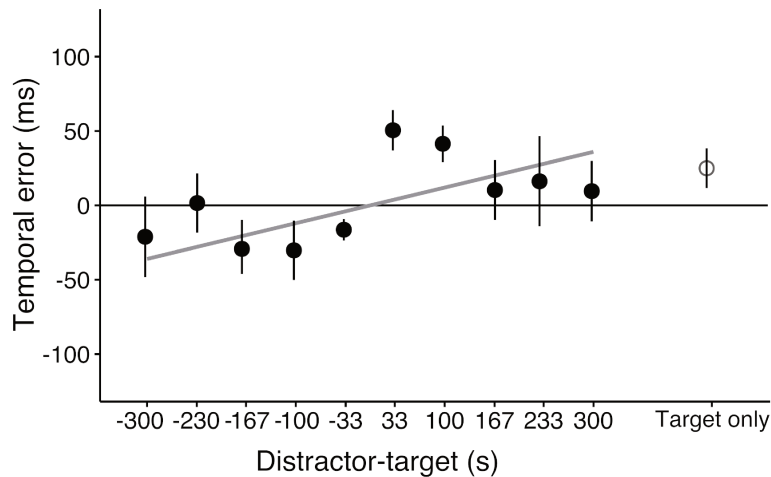


FIGURE 3.5: Attraction to the timing of the distractor in the *post-cued by color* experiment, in which duration of the trial was 1.5 seconds. Average temporal error across participants is plotted against different temporal delays between distractor and target. As in the other *post-cued by color* condition, the reported time of the target was biased to the moment when the distractor was presented. However, the distractor had an effect in more narrow temporal interval than (-100 to 100 ms) when trial lasted 1.5 seconds, compared to the 2 seconds. Temporal error in condition where only one stimulus was presented is shown in open symbol. Black line is the linear mixed-effect model fitted to the data. Error bars correspond to standard error of the mean.

we found an interaction between the temporal order between target and distractor and the cueing method. The order between target and distractor had a different effect depending on the cueing method (for *pre-cued by color*:  $b = -0.07316$ ,  $SE = 0.0360$ ,  $t = -2.05$ ,  $p < 0.05$ ; for *pre-cued by order*:  $b = -0.1753$ ,  $SE = 0.035$ ,  $t = -5.013$ ,  $p < 0.01$ ). Excluding the interaction of the two predictors decreased the goodness-of-fit, as quantified by a comparison of log-likelihoods of the two models by means of Chi-square test (Chi-square (2) = 25.648,  $p < 0.01$ ). A Wilcoxon one-sample test revealed that there was no bias observed when only one stimulus was presented in the *pre-cued by color* experiment ( $V = 15$ ,  $p = 0.74$ ).

### 3.5 Discussion

The moment when a target is perceived is biased by the presentation of other events in near temporal proximity, and this bias differs depending on the expectation of the observers. When participants attend equally to both the target and a distractor, which is necessarily what happens when the target is revealed at the end of the trial, the reported time of the target is attracted towards that of the distractor. This finding is in general agreement with previous works on the effects of temporal context on duration judgments (Burr et al., 2013; Nakajima, Ten Hoopen, et al.,

1992; Sawai et al., 2012). The difference between these previous studies and the present one is that we find an effect of temporal context on the perceived time for a single brief event rather than an extended duration. Attending to one stimulus of the pair revealed a different effect of the distractor on the reported time of the target. Interestingly, the reported time depended on what is being attended. When participants knew beforehand the color of the target to be presented, the target was reported earlier than when it was actually presented. Conversely, when the temporal order of the target was the cue to identify target and distractor, the target was reported later. At this stage, we can only speculate on the reasons why attending to color or temporal order creates different biases. It is known that humans sometimes fail to properly monitor the duration of certain perceptual processes or motor actions. For example, the duration of saccades or attentional shifts are inaccurate (Jonikaitis, Deubel, & De'Sperati, 2009; Morrone, Ross, & Burr, 2005), although the duration can be compensated for later (Yarrow et al., 2001, 2006). Similarly, durations of blinks are ignored (Duyck, Collins, & Wexler, 2015; Riggs, Volkman, & Moore, 1981). Our findings in the *pre-cued by color* experiment could be explained by an underestimation of the time needed to process the color of the distractor, or make an inference about which of the two stimuli is the one that has the cued color. Unlike attending to the color of the target, cueing the temporal order of the target does not require processing of the distractor stimulus. When an event is known to be a distractor even before it appears (*pre-cued by order*), the time needed to process it is overestimated, and the target is reported later. Importantly, no bias was observed when only the target was presented in the *pre-cued by color* experiment, confirming that the distractor is necessary for the effect. Unfortunately, the corresponding condition where only the target was presented cannot be run in the *pre-cued by order* experiment, and so we cannot confirm that the bias disappears in this condition. In summary, we found that the perceived time of a single brief event can easily be biased to appear earlier or later than when it was presented. Interestingly, this perceived time is determined by the manner in which we attend to the other events presented before or after that event.

## 3.6 Conclusions

In this chapter I presented findings from a series of experiments in which I explored how the perceived time of visual events depends on the other events in their temporal proximity. When participants did not know in advance which of the two stimuli they would be asked to report, the perceived time was biased towards the timing of the distractor. These findings suggest that biases arise from sequential encoding and/or maintenance of temporal information. The motivation for the experiments in which the target was pre-cued was to disentangle between the perceptual and memory effects. The hypothesis was that if the attraction bias had an early sensory locus, it would persist regardless of the knowledge about the target identity. When the target was pre-cued, by its color or temporal order, the attraction towards the timing of the distractor was no longer found. Nevertheless, the perceived time was still affected by the manner in which the other event in the target's temporal proximity was processed. The effects of distractors on the perceived spatial position of a visual event is different depending on the temporal order between the target and the distractor (Chien et al., 2011; Chow et al., 2014; Ono & Watanabe, 2011; Suzuki & Cavanagh, 1997). It is an open question whether a similar dissociation can be found for the biases reported here, notably in the *pre-cued by order* experiment.



## Chapter 4

# The Perceived Time of Multisensory Events

In the previous chapter I presented the project investigating how the perceived time of a visual event is affected by other stimuli presented before or after it. The findings indicate that the perceived time of the stimulus was biased towards the other event, in a condition in which participants did not know in advance which of the two stimuli they will be asked to report. When the target was cued beforehand, the reported time was under or overestimated, depending on whether the nature of distractor had to be decoded (pre-cued by color) or not (pre-cued by order). In the project presented here, the interactions between the perceived time of auditory and visual events were investigated. More specifically, are there mandatory interactions for the perceived time of auditory and visual events, for a wide range of asynchronies?



## 4.1 Abstract

Temporal coincidence of events is an important cue for multisensory integration. Even though the brain accommodates timing differences between senses (Fujisaki et al., 2004; Vroomen et al., 2004), underlying mechanisms are still not completely understood. In the work reported here we investigated whether there are mandatory interactions between the two modalities for perceived time of events. Stimuli had varying magnitude of asynchrony between the senses. Participants estimated the time of the stimuli onset following a self-paced key press. They were explicitly asked to attend to only one modality, ignoring the other sensory event. For the range of synchronies tested, the perceived time of the stimulus from the attended modality was affected by the asynchronous stimulus from the other modality, indicating mandatory interactions between the two modalities.

## 4.2 Introduction

An auditory and a visual signal coming from the same event are almost never physically synchronous. The transmission delays on the receptor level (Tyler, 1985), as well as delays at different stages of processing (Heil & Irvine, 1997; Raij et al., 2010) are different for the two modalities. Nevertheless, the difference in processing times, as well as the small physical lags between the signals are difficult to detect (Hirsh & Sherrick, 1961; Keetels & Vroomen, 2005; Vidal, 2017; Zampini et al., 2005, 2003). The range of physical asynchronies for which the signals are integrated, known as the temporal window of integration, can be quite large for the auditory and visual signals. It depends on the stimulus complexity, task, and stimulus layout (Hirsh & Sherrick, 1961; Love et al., 2013; van Wassenhove et al., 2007). In addition, even when the asynchrony between the signals is large, the moment when one signal is perceived can be biased by the timing of the other signal (Roach et al., 2006; Vidal, 2017). In the work reported here, we investigated whether these interactions between modalities are mandatory. In particular, when we estimate the time of an event in one modality, can we ignore an asynchronous signal from another modality?

Previous work suggests that unattended, asynchronous events can bias the perceived time of attended ones. For example, in a rate discrimination task, rate estimates of rapid intensity modulations of a visual or auditory signal are affected by the conflicting rate of stimuli in the unattended modality. In addition, the effect decreases with increasing conflict between the attended and unattended stimuli (Roach et al., 2006). When the discrepancy between the signals is very large, no

bias is observed (Roach et al., 2006). The results were explained by a Bayesian model, in which the likelihoods of the two signals are combined with prior knowledge about the probability of correspondence between the two signals. When the reliability of the visual and the auditory signals is equal, there is a symmetrical influence of one on the other. On the other hand, when the auditory stimuli are less reliable, the bias induced by vision is more pronounced. In order to quantify shifts in the perceived time of the unisensory signals when signals from another modality are presented in their temporal proximity, Vidal (2017) presented sequentially four pairs of auditory and visual stimuli, followed by the fifth, unimodal stimulus (visual or auditory). The asynchrony between the auditory and visual stimuli was varied, and a wide range of asynchronies were tested (up to 200 ms). In separate blocks, participants were asked to estimate the rate of either the visual or auditory stimulus. The task was to respond as to whether the unisensory stimulus was presented sooner or later, relative to the regular rhythm between the first four events. The study provided several important insights. When the signal reliabilities were matched, both the auditory and visual stimuli estimates were affected by the timing of the stimuli from the other modality. However, in order to match the reliabilities of the signals, the signal to noise ratio of the auditory stimulus had to be very low. Furthermore, the effect depended on the order between the stimuli. More specifically, the perceived time of the attended stimulus was attracted towards the signal from the other modality when the unattended one was presented presented after, but not when it was presented before, the attended one. It should be noted that in order to reduce serial effects, the asynchronous audiovisual pairs were presented four times on each trial, before the unisensory target. Although the repetition of the audiovisual stimuli with fixed asynchrony in each trial reduced the effects of the previous trials on the perceived time of the multisensory events, it possibly lead to a fast recalibration (van der Burg et al., 2015; van der Burg et al., 2013). Since the same asynchrony was presented multiple times, the fast adaptation could lead to an overestimation of the attraction effect within a single pair of signals in this study.

In the work reported here, we investigated the multisensory temporal interactions in a single audiovisual stimulus, for a wide range of asynchronies. In two separate blocks, participants estimated elapsed time from the onset of the trial to the presentation of an auditory or a visual stimulus. The onset of the temporal interval was marked by self-paced key press, and the offset was marked by an audiovisual stimulus. In separate blocks, participants were asked to attend only to the visual (*attending to vision* condition) or auditory (*attending to audition* condition) stimulus, and ignore the stimulus from the other modality. We tested a range of

asynchronies (from synchrony, to the auditory stimulus leading, or lagging the visual for 200 ms) in order to investigate how the multisensory interactions change with the temporal lag between the two signals.

## 4.3 Method

### 4.3.1 Stimuli and apparatus

The stimuli were presented via a custom built device consisting of green light emitting diodes (LED) placed on top of a loudspeaker. The LEDs were arranged in a square, subtending 3 dva at a viewing distance of 40 cm. The visual and auditory stimuli were delivered by two different audio channels, which ensured an accurate timing of both the auditory and visual stimuli. The experiments were created using Matlab R 2016a and Psychtoolbox-3 (Brainard, 1997; Kleiner et al., 2007). The auditory stimulus was a 20 ms burst of pink noise at sampling rate 65 kHz, loudness 70dB, delivered from the loudspeaker placed underneath LEDs. The viewing distance was 40 cm.

### 4.3.2 Procedure

The task was a self-paced temporal bisection task. On each trial participants estimated the duration of the temporal interval, and compared it to previously learned references (*short* and *long*). The onset of the interval to be timed was marked by a self-paced key press. The offset of the interval was marked by an audiovisual stimulus. At the beginning of the experiment, and after each break, two reference durations (250 and 1050 ms) were presented 10 times. In the exposure phase, the auditory and the visual stimuli were always synchronous (Figure 4.1A). In two blocks in the main part of the experiment, participants estimated the duration of the temporal interval between their keypress and the visual or auditory stimulus. Participants compared the estimated duration to the two memorized reference durations, and reported whether the duration between the keypress and the stimulus was more similar to the short or the long reference. Before the start of the experiment, participants completed 30 trials of training with feedback.

To investigate how the temporal conflict affected the estimated time of the stimulus, we varied the asynchrony between the auditory and visual stimuli in seven linearly spaced steps (auditory stimulus leads or lags the visual stimulus for 200, 130, or 67 ms, and a synchronous condition). We varied the duration between the keypress and the stimulus in six logarithmically equally spaced steps (250, 330,

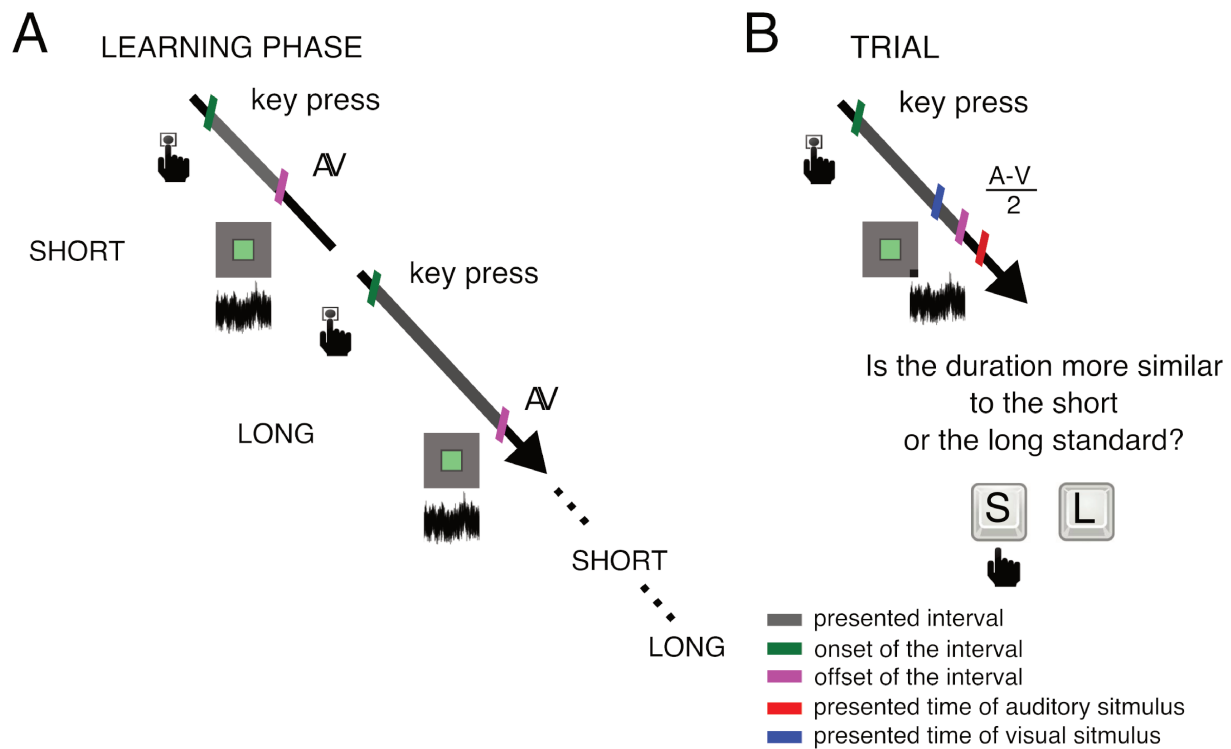


FIGURE 4.1: Illustration of one the learning phase (A) and a trial sequence (B) (A). In the learning phase, the two standard durations, short (250 ms) and long (1050 ms), are repeatedly presented. The duration onset is marked by a self-paced key press. The offset of the duration is marked by the audiovisual stimulus. In the learning phase, the auditory and visual stimuli were always presented synchronously. (B). A trial starts with a self-paced key press. After a variable delay, the auditory and visual stimuli are presented. The duration of the interval was centered in the middle between the two signals. The participant's task is to estimate the duration between the key press and one of the two stimuli. In separate blocks, participants reported the duration relative to the onset of the visual or the auditory stimulus. Seven stimulus onset asynchronies were tested (the difference between presentation time of the auditory and visual modality from -200 to 200 ms). Six different durations were presented in each asynchrony condition.

440, 600, 790 and 1050 ms). By convention, the presented interval was centered in the middle between the auditory and visual stimuli. For example, if the presented interval was 600 ms, and the asynchrony condition 200 ms, the visual stimulus was presented 500 and the auditory stimulus 700, after the participant-initiated keypress. Therefore, if the two signals were integrated with equal weights, there would be no difference in responses for different asynchrony conditions. On the other hand, if the perceived time of the signal in one modality was not affected by the time of the other stimulus, the percept is going to be driven by the attended modality.

In the two blocks, participants were asked to attend to only one modality, and

ignore the other stimulus. For each multisensory condition, there were seven asynchrony conditions (7 stimulus onset asynchronies) of 180 trials (6 interval durations and 30 repetitions).

### 4.3.3 Participants

Seven participants, including the author participated in the study. Participants had normal or corrected-to-normal vision and reported normal hearing. All participants but one were naive to the purpose of the study and gave written informed consent. The experiment was conducted in agreement with the Declaration of Helsinki and the local ethics regulations.

## 4.4 Results

For each interval duration and asynchrony condition, we obtained the frequency of trials the stimulus was estimated to be more similar to the long reference. The data for one participant are shown in Figure 4.2.

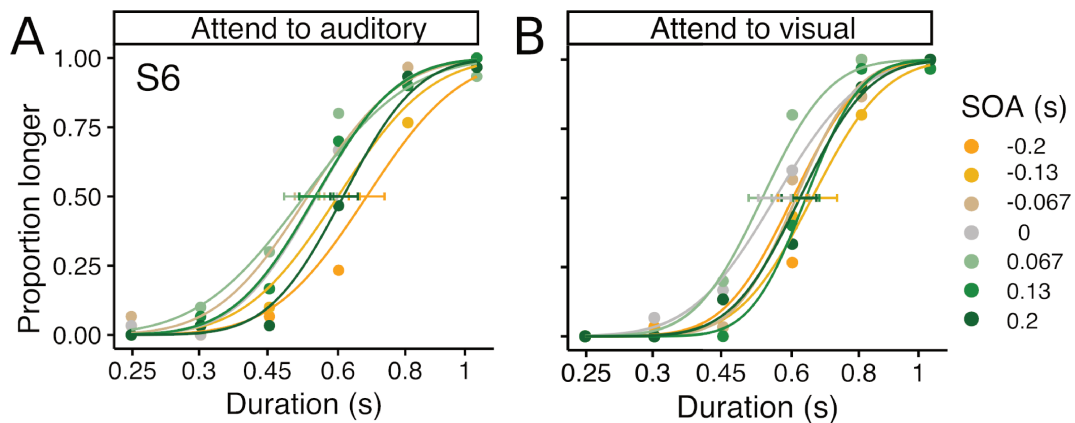


FIGURE 4.2: Proportion of *longer* responses against the presented duration for one participant. Continuous curves represent fits of cumulative Gaussian distribution to the data. The different asynchrony conditions are color coded. The negative asynchronies (different shades of orange) are conditions in which the auditory stimulus preceded the visual, and positive asynchronies (different shades of green) are conditions in which the visual stimulus was presented first.

To estimate performance in the task we fitted cumulative Gaussian distribution to participants' responses, for each participant and condition separately. Since participants were free to adopt a criterion to categorize the short and long intervals (we will refer to this value as the Point of Subjective Equality or PSE), we centered individual PSEs to the PSE in the condition in which the auditory and visual signals were presented synchronously. Since all the conditions were randomized during

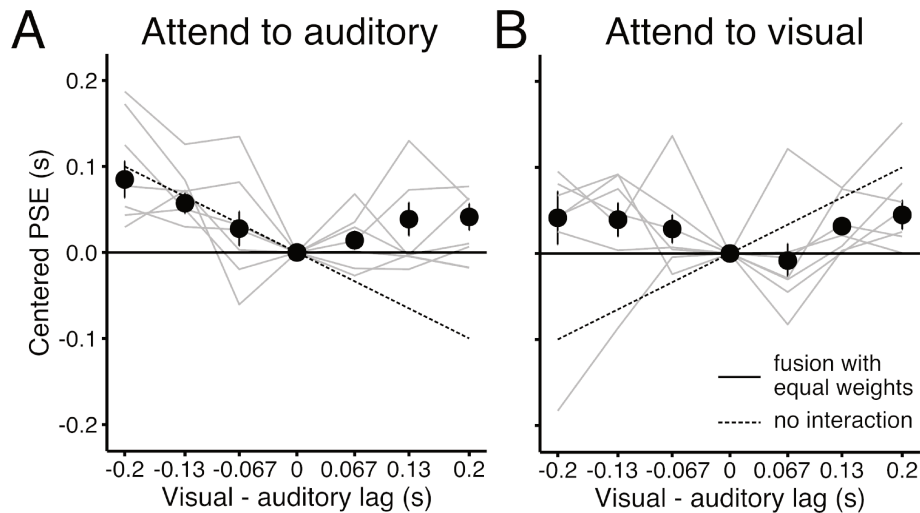


FIGURE 4.3: The average centered PSEs for different tested lags. The PSEs are centered to the condition in which the auditory and visual signals were synchronous. (A) Biases when participants were asked to report the duration of the auditory stimulus. The average centered PSEs are plotted against the lag between the auditory and visual stimuli. (B) Biases when participants were asked to report the duration of the visual stimulus. The average centered PSEs are plotted against the lag between the auditory and visual stimuli. The average data are shown in black symbols, and individual data in gray lines. Error bars correspond to the standard error of the mean between participants. Dashed lines indicate where the PSEs would be if participants would ignore completely the stimulus from the other modality and always respond according to the signal from the attended modality. The complete fusion of the visual and auditory signal with equal weights would lead to no change in the PSE with asynchrony, as indicated by the continuous horizontal line.

the experiment, we assumed that the criterion participants adopted was the same for different magnitudes of asynchrony between the signals. The average centered PSEs are plotted against the asynchronies for the two conditions in Figure 4.3.

The perceived time of the auditory and visual stimuli depended both on the lag between the two stimuli, as well as whether the attended stimulus was presented first or second. On average, when participants attended to the auditory stimulus, and the auditory stimulus was presented first (Figure 4.3A), participants' PSEs depended on the asynchrony between the two signals. This pattern of results indicates that participants succeeded to ignore the visual stimulus, and their judgements were only affected by the physical timing of the auditory stimulus. On the other hand, when the unattended stimulus (visual) was presented before the attended stimulus (auditory), PSEs were similar regardless of the asynchrony between the two stimuli, indicating that participants now integrated the two sensory modalities. A similar pattern of results was found for the condition in which participants attended to the visual stimulus (Figure 4.3B). However, as shown by

individual the PSEs on Figure 4.3, there was considerable variability between participants.

We tested whether the centered PSEs in different SOA conditions were different across the conditions by means of two Friedman's test. For PSEs in the auditory condition, the Friedman's test indicated a significant difference (Friedman chi-squared (6) = 15.673,  $p < 0.05$ ), meaning that the PSEs for the auditory stimulus were affected by the lag between the two signals. However, no pairwise comparisons were significant (Wilcoxon test, with Bonferroni correction for multiple comparisons). In the condition in which participants attended to the visual modality, there was a significant difference between the PSEs for different lags (Friedman chi-squared (6) = 14.633,  $p < 0.05$ ), but no significant contrasts.

## 4.5 Model

When asked to discriminate the durations between a self-paced key-press and the auditory or visual stimuli, participants estimates were affected by the asynchronous timing of stimulus in the unattended modality. In order to describe the mechanism of the temporal interactions of signals from the two modalities, we fitted different models to the data.

### Maximum likelihood estimation

The maximum likelihood estimation (MLE) model of multisensory integration proposes that signals from different modalities are combined in a statistically optimal manner. In particular, the multisensory estimate is a weighted sum of the two unisensory estimates, weighted by their reliabilities. The weights correspond to the inverse of the variability of individual estimates. Integrating different cues in this manner yields estimates that have reduced uncertainty compared to unisensory signals. A great body of work found that unisensory cues are combined according to the MLE rule both between (Alais & Burr, 2004; Ernst & Banks, 2002; Gepshtein & Banks, 2003) and within sensory modalities (Hillis et al., 2002a; Knill, 2003; Landy & Kojima, 2001). It is not clear, however, whether the signals from different modalities are combined in this optimal manner for estimating the time of events. In particular, auditory dominance is greater than expected from unisensory variabilities (Burr et al., 2009), and no reduction in multisensory variability has been found (Hartcher-O'Brien & Alais, 2011).

### The partial integration model

In order to explain how the signals from different modalities interact for a wide range of conflicts between modalities, different partial integration models have been proposed (Adams, 2016; Ernst, 2006, 2007; Roach et al., 2006). In particular, unlike in the MLE model, in which the signals from the two modalities are always integrated, these models propose flexibility in the integration process. For example, Ernst (2006) proposed a coupling prior that is combined with the likelihoods to obtain the posterior estimate of the dimension of interest (e.g. size, tilt or time). The coupling prior determines the integration strength: the wider the prior distribution, the more stimuli with greater conflict are integrated. Here we considered a variant of the partial integration model. Instead of modeling the coupling prior with free parameters in the model, we tested whether simultaneity judgements can serve as an underlying rule of combination. In particular, we obtained simultaneity judgements from six participants in a separate experiment, for the seven asynchronies tested in the main experiment. Then, we used the probability of judging a certain temporal asynchrony between auditory and visual signals as synchronous as an estimate of probability that the two signals will be fused. In other words, the two signals were fused according to the MLE rule with probability  $p_{\text{synchronous}}$  and segregated with probability  $1 - p_{\text{synchronous}}$ , with different  $p_{\text{synchronous}}$  for each asynchrony level. When signals are not fused, the estimate is made only based on the unisensory signal from the attended modality. This model has four free parameters: the two sensory uncertainties, and the decision criterion and variability. In addition, we considered a more complex model, to account for the asymmetry of the effect observed in the data (Figure 4.3). In this version of the model, the uncertainty of encoding of the attended stimulus is reduced when the attended stimulus is presented before the unattended one (the partial integration model with asymmetric weights).

### **The focal switching model**

According to the focal switching model (Adams, 2016), on each trial, two unisensory estimates are made. The decision is made by comparing the unisensory signal from the attended, or unattended modality against the criterion. The probability of *switching* to the estimate in the unattended modality is a free parameter in the model, in addition to the two unisensory variances and the decision criterion and uncertainty. As for the partial integration model, we also considered a more complex model, in which participants can switch modalities with different probability, depending on whether the attended modality is presented first or second.

### **No multisensory interactions: attended or unattended modality estimates**



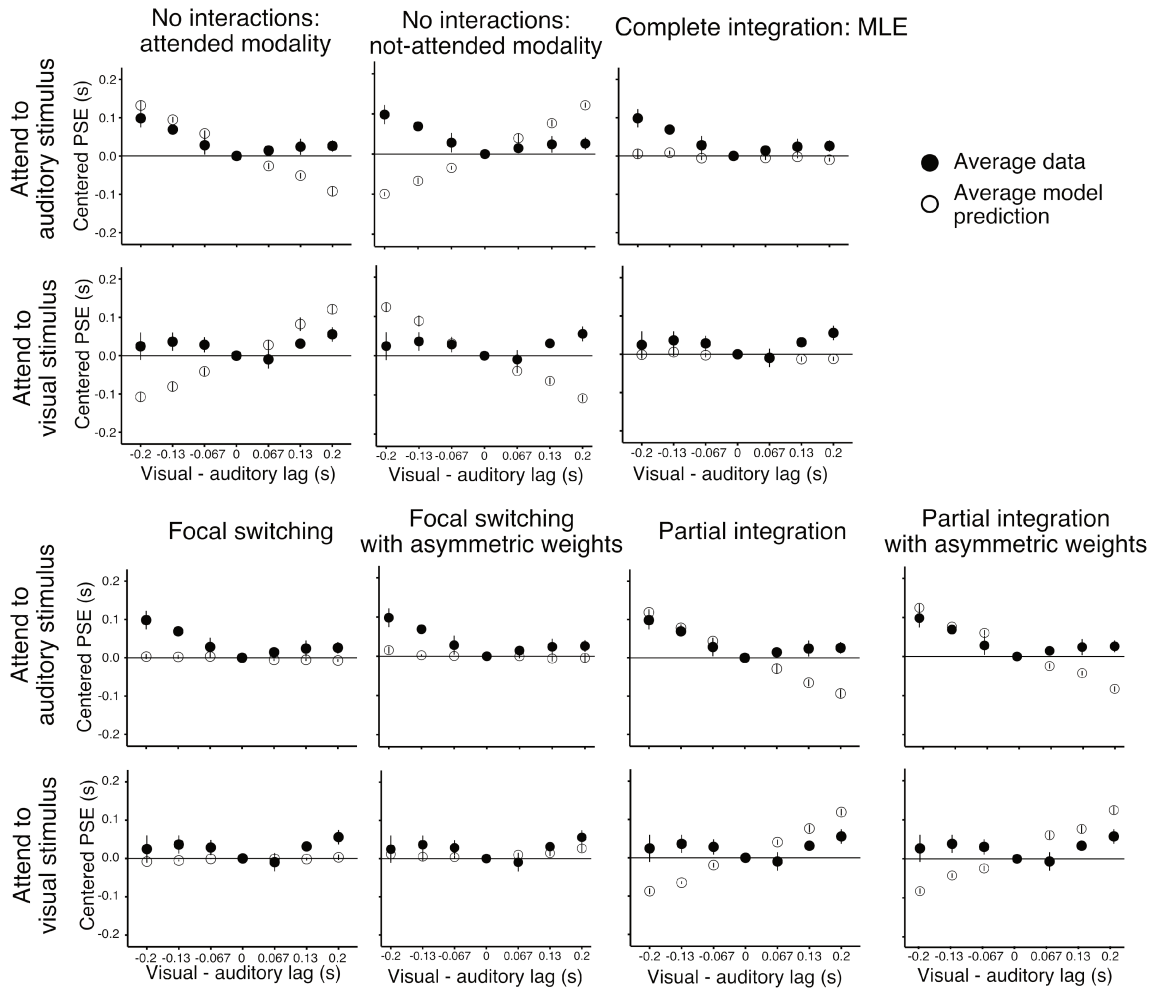


FIGURE 4.4: The average predicted PSEs for different tested models and average observed PSEs. Each panel shows different model predictions (open symbols), superimposed on the data (filled symbols).

These two models are the extreme cases, in which signals from the two modalities do not interact for estimating time of the unisensory events. In the *attended modality* model, there is no effect of the unattended modality, and the estimate always corresponds to the signal from the attended modality. Conversely, in the *unattended* modality, participants make a decision based on the signal from the not-attended modality only. These models have three four parameters, the auditory and visual variances, and the decision criterion and variability.

## 4.6 Model comparison and selection

We selected the models that describe the data the best in two steps. First, we used a qualitative approach, and we retained only models that qualitatively described the data well. The predictions from the different models are shown in Figure 4.4.

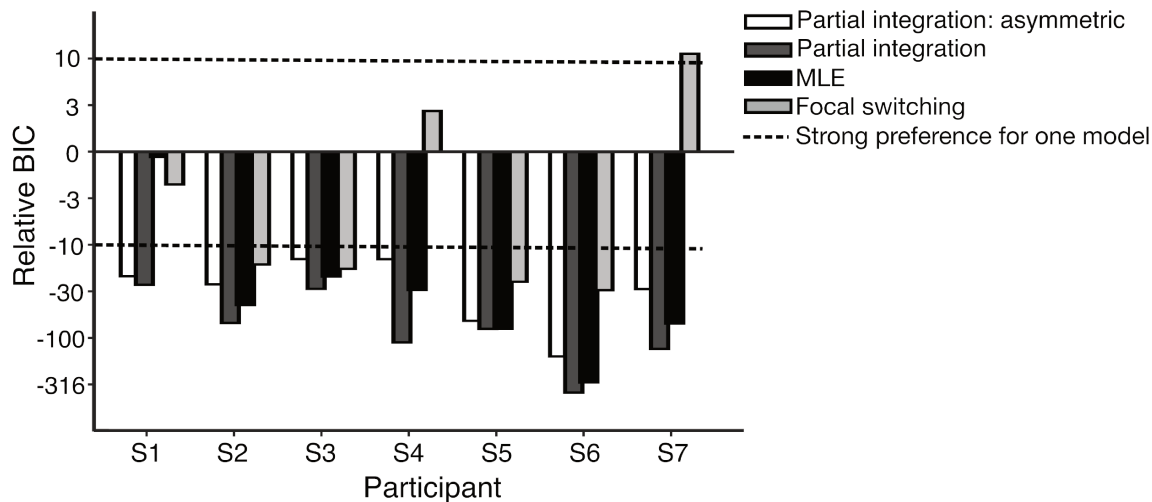


FIGURE 4.5: Quantitative model comparison. The difference between the best model (*focal switching model* with asymmetric weights) and other models is shown for each subject. Two horizontal lines correspond to a value of BIC that is considered to be a significant improvement of one model fit to the data relative to the other (Jarosz & Wiley, 2014).

As shown in Figure 4.4, models that do not assume any interactions between modalities clearly fail to qualitatively capture the trend in the data. Next, we compared the likelihoods of different models, by means of the Bayesian Information Criterion (BIC, Jarosz and Wiley (2014)). Since there was some variability between participants, we calculated a difference in BIC between the model that was overall the best fit to the data, the *focal switching model* with different weights depending on the order of the attended and unattended stimulus. For all participants, both the *partial integration* and the *partial integration with asymmetric weights* models were significantly worse than the focal switching model. The *MLE* model was worse for all but one of the participants. Finally, the *focal switching model* was better for one participant and equally good for another. In summary, the focal switching with or without asymmetric weights appear to best account for the data.

## 4.7 Discussion

In the work presented here we investigated whether the perceived time of events is biased by events from another modality presented in temporal proximity. Participants estimated durations between a self-paced key-press and the auditory or visual stimuli. The stimulus in the attended modality was presented before, after, or in synchrony with the stimulus from the other modality. Participants responded as to whether the duration between the key press and the attended stimulus was

more similar to a long or short reference, learned at the beginning of the experiment. We found that participants still integrated information from the unattended modality: the PSEs were affected by the timing of the other signal. These effects are in agreement with the previous work, showing that perceived the rate (Roach et al., 2006) and rhythm (Vidal, 2017) of both auditory and visual events can be biased by asynchronous events from another modality. Here we showed that the interactions between modalities also exist for a single audio-visual pair.

We used modeling to describe possible mechanisms of observed interactions between the modalities. We compared observed performance to different models. Not every participant's data was best explained by the same model. However, for each participant, the best model included interactions between modalities. The difference between the tested models is how the interactions are realised. For most of participants, the best model was *focal switching model*, with asymmetric switching probability. The switching probability was different depending on whether the first stimulus was presented the first or the second. However, as shown on Figure 4.5, the likelihood of other models, was not always considerably lower for some participants.

In summary, the findings reported here indicate that multisensory interactions for perceiving the time of events are mandatory for a wide range of asynchronies. The modeling confirmed that the behavior of participants is well described by assuming the interactions between modalities. In addition, the best models included an asymmetry in the effect: the perceived time of an event was more affected by the asynchronous events from another modality if it was presented after the unattended events. The asymmetries in the effect of the distractor have been previously reported (Vidal, 2017; ?). However, the effects reported in earlier studies were in the opposite direction: the perceived time was more affected by an another event that presented after the stimulus. Therefore, the mechanisms underlying these biases might not be the same. However, further work is needed to specifically address this question.

## 4.8 Supplementary experiment and data

### 4.8.1 Simultaneity judgements

Six participants completed a simultaneity judgement task. We presented the same temporal lags between the auditory and visual stimuli. The participant's task was to report whether the two stimuli were presented simultaneously or not. The proportion of trials in which the two stimuli were reported to be simultaneous is plotted against the tested stimulus onset asynchronies in Figure 4.6.

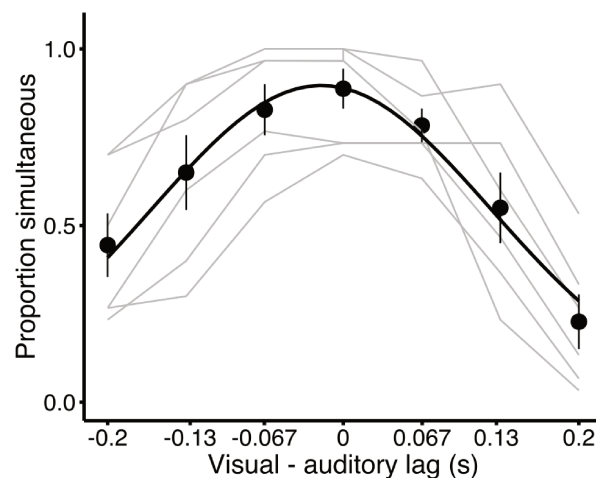


FIGURE 4.6: Results of a simultaneity judgement task. Participants were presented with auditory and visual stimuli with a temporal lag between them varying from trial to trial. Average proportion of trials in which the two signals were judged as simultaneous is plotted against tested lags. Average data across six participants is shown in black symbols. Gray lines show individual data, and black continuous line is a Gaussian distribution fit to the data.

## 4.8.2 Unisensory sensitivity

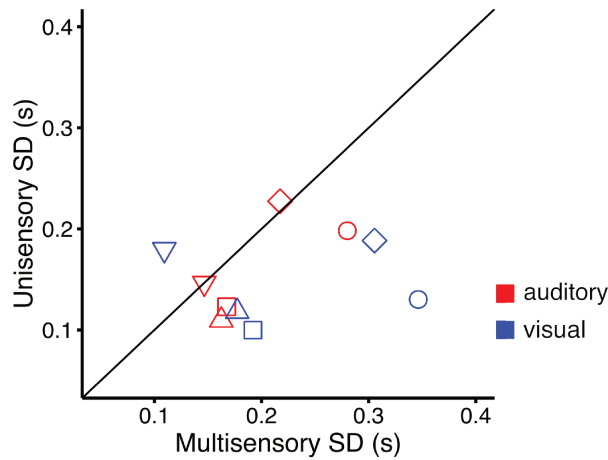


FIGURE 4.7: Unisensory standard deviations plotted against the multisensory standard deviations in the two conditions (*attending to visual* and *attending to auditory*). The modalities are color coded, red symbols correspond to auditory and blue to visual conditions. Each symbol data from one participant.

For five out of seven participants we also tested performance in unisensory tasks. The standard deviation of fitted cumulative Gaussian functions for the two modalities are plotted (color coded) against the standard deviation in the multisensory experiment, for the condition in which the two stimuli were synchronous (separately for *attending to visual* and *attending to auditory* conditions). There are two important aspects of the unisensory performance that should be noted. First, the performance for the stimuli in the two modalities was comparable. Second, the unisensory uncertainty of discrimination was consistently lower than those in the multisensory condition. These lower thresholds for unisensory conditions are not consistent with cue combination following the MLE rule. One possibility is that instruction to participants to attend to only one modality changed the manner in which the two signals were encoded and integrated (Spence & Parise, 2010). Alternatively, the cue combination between auditory and visual signals for estimation of time is not optimal in MLE sense, which has been shown in the previous work (Burr et al., 2009; Hartcher-O'Brien & Alais, 2011). The both interpretations indicate that MLE rule is not mandatory for combination of auditory and visual information for time estimation.

## 4.9 Conclusions

In this chapter, I investigated the multisensory temporal interactions between asynchronous stimuli. Participants estimated elapsed time from the onset of the trial to the presentation of an auditory or a visual stimulus. In separate blocks, participants were asked to attend only to the visual or auditory stimulus, and ignore the stimulus from the other modality. For the range of synchronies tested, the perceived time of the stimulus from the attended modality was affected by the asynchronous stimulus from the other modality.

There was, however, variability between participants, also reflected in the modeling of the effects: for the models we tested, there was no single model that described the performance of all of the participants better than others. That said, for all participants the models that include some interactions between the modalities described the data better than the models with no interactions. The task used in this study was a variant of the temporal bisection task, which allowed testing interactions in a single audiovisual pair, rather than the rhythm between multiple stimuli (Burr et al., 2009; Vidal, 2017). In order to investigate when a target is perceived, we need to ask participants to estimate that moment relative to some reference. Previous studies used other visual and auditory stimuli as references (Burr et al., 2009; Hartcher-O'Brien & Alais, 2011; Vidal, 2017). Here, the self-paced key press was used, as a neutral reference relative to the two tested modalities. However, it is possible that this choice introduced additional variability or bias. Given the small number of participants in the study, it would be imprudent to further speculate on the origin of the variability. However, it has previously been shown that different subjects can adopt different strategies, or rules for integrating cues from different modalities (Adams, 2016; Locke & Landy, 2017; Wozny, Beierholm, & Shams, 2010). Further work is needed to investigate the origin of these effects.

In summary, the work presented so far showed that temporal context biases the perceived time of visual and auditory events. In the next chapter, I will present studies investigating how spatial context affects the perceived time of visual events.



## Chapter 5

# When an event is perceived depends on where it is presented

In the previous chapters I presented work investigating how the perceived time of events is biased by other, asynchronous events. Events from the same and different modality biased the perceived time of events. In addition, the manner in which the events were attended to affected the perceived time, revealing a complex relationship between attending to stimuli and their perceived time. The evidence about how perceived duration and relative time depend on the location of the stimulus in the visual field is scarce (Aedo-Jury & Pins, 2010; Kliegl & Huckauf, 2014; R. Rutschmann, 1966). To further explore this question, I conducted a series of experiments presented in this chapter.



## 5.1 Abstract

Temporal processing is not uniform across the visual field. Perceived relative time and duration depend on the position of the stimulus in the visual field (Aedo-Jury & Pins, 2010; Kliegl & Huckauf, 2014; Poffenberger, 1912; R. Rutschmann, 1966). In addition, the speed of visual processing is greater in the periphery (Carrasco, McElree, Denisova, & Giordano, 2003). Here we investigated when events are perceived across the visual field. Participants were initially familiarized with a fixed interval duration by watching the hand of a clock rotating at a constant speed, making one full revolution in 2 seconds. In the main part of the experiment, the hand was removed and a pair of small discs was briefly flashed at a random time within the interval duration. Participants used a cursor to indicate the location where the hand would have been at the time of the flash. In different blocks of trials, the discs were presented at different eccentricities from 0 to 18 dva. To minimize attentional redirection to one hemifield, two stimuli were simultaneously presented on either side of fixation. Events were perceived earlier when they were presented in the periphery rather than at fixation. A bias of around 100 ms was present for stimuli. In a series of subsequent experiments, we investigated possible origin of this bias.

## 5.2 Introduction

How humans estimate when an event has happened is still not well understood. This question is usually addressed in the context of the perceived time of one event relative to another, known as *relative time* (Arnold, 2010; Roufs, 1963). The most straightforward hypothesis is that the perceived time is related to the processing of the stimulus, and that events are perceived when processing of some aspect of the stimulus is completed (Moutoussis & Zeki, 1997b; Roufs, 1963). For example, there is a correspondence between the duration of exposure needed to detect binocular disparity changes of different magnitude, reaction time to those changes, and their perceived temporal order (Arnold & Wilcock, 2007). Since it is known that binocular information is not integrated before the cortex, these findings are interpreted as evidence that the perceived time of events depends on the time course of the cortical processing of stimuli.

However, this correspondence between reaction times and temporal order judgments is not always found. For example, in certain conditions, humans will estimate a dimmer stimulus to have occurred first (Bachmann, Pöder, & Luiga, 2004b), even though visual latency is greater for low luminance stimuli (Williams & Lit, 1983). Furthermore, even when perceptual latencies are estimated with a reaction

time task and temporal order judgements are in the same direction, the magnitude of the latencies estimated in the two tasks can be different (Cardoso-Leite et al., 2007; Tappe et al., 1994). For example, it has previously been shown that temporal order judgements for events presented at the fovea and in the periphery (30 dva) are biased (R. Rutschmann, 1966). Participants are at chance for discriminating the relative time between peripherally and centrally presented events, when the peripheral event is presented earlier, indicating that peripheral events are perceived later than central ones (on average, about 70 ms before). Similarly, reaction time is slower for stimuli presented in the periphery (Osaka, 1976; Poffenberger, 1912). The effect of peripheral presentation on reaction time is smaller than that found using temporal order judgements, although it varies across the studies (10ms in Poffenberger, 1912; 15ms in Ando et al., 2001, but up to 40ms when order of presentation was randomized in Osaka, 1976). These results are interpreted in terms of processing latencies: stimuli presented in the periphery are processed slower, and therefore, perceived later. However, it is not always the case that processing in the periphery is slower compared to that in the center of the visual field. For example, a series of studies showed that the speed of processing in a visual search task is faster when stimuli are presented at peripheral locations (Carrasco, Giordano, & McElree, 2004, 2006; Carrasco et al., 2003). In addition, a human magnetoencephalography study showed that visual cortical activations are faster for stimuli presented in the periphery compared to the fovea (Stephen et al., 2002).

Here, we investigated *when* events are perceived at different positions in the visual field. We asked participants to estimate when stimuli were presented, relative to the onset and offset of a trial, rather than other stimuli presented in temporal proximity of the test stimulus. At the beginning of the experiment, participants were shown a fixed duration of one trial, by watching the hand of a clock rotating at a constant velocity. In the main part of the experiment, the hand of the clock was removed, and participants were asked to attend to the time from the onset to the offset of the trial. A white disc was flashed briefly at different locations on the horizontal meridian. At the end of the trial, participants indicate where the hand of the clock would have been at the time of the flash. To investigate whether the reported time depended on the position of the stimulus in the visual field, in Experiment 1 we presented stimuli at ten different locations along the horizontal meridian.

### 5.3 Experiment 1

The aim of this experiment was to investigate whether the moment when an event is reported is affected by its location in the visual field. To investigate when an

event is perceived, we adopted the procedure previously used to investigate the timing of a conscious decision (Libet et al., 1983), that has already been described in the previous chapter.

### **5.3.1 Method**

#### **5.3.1.1 Stimuli**

The stimulus was a white disc of radius 2 dva, flashed briefly (33 ms) at different positions on the screen. The fixation point was a 1 dva white disc that changed its luminance to dark gray as a preparation signal, just before the beginning of the trial. The hand of the clock had a radius of 2.5 dva and also white. Each trial started and ended with a 33 ms pure tone of frequency 1 kHz.

#### **5.3.1.2 Apparatus**

The experiment was conducted in a dimly lit room. Experiments were created using Matlab R 2016a and Psychtoolbox-3 (Brainard, 1997; Kleiner et al., 2007). Stimuli were presented on a LCD flat screen (ViewSonic V3F245), with diagonal 24 in, resolution 1920 × 1080 pixels, and refresh rate 60 Hz. The viewing distance was 30 cm. The analysis of the data was conducted in the R Studio environment, using packages “lme4” (Bates et al., 2014) and “lmerTest” (Kuznetsova et al., 2017) for mixed effect regression analysis. We excluded trials with an error greater than 120 degrees from the analyses (less than 5% of the trials were excluded).

#### **5.3.1.3 Participants**

Eight participants (two male) took part in the experiment, with mean age, 24 years. All but one of the participants (the author) were naive to the purpose of the experiment and gave written informed consent. The experiment was conducted in agreement with the Declaration of Helsinki and the local ethics committee.

#### **5.3.1.4 Procedure**

At the beginning of the experiment, participants were familiarized with a fixed trial duration by watching the hand of a clock rotating at a constant speed, one cycle in 2 seconds. During the main experiment, only the fixation was presented for most of the duration of the trial, and participants were asked to fixate at the center of the screen during the trial. At the beginning and end of the trial, two brief tones (33 ms, 1 kHz) were presented, in order to provide additional cues for trial onset and offset. A stimulus was flashed at a random time between the beginning and

the end of the trial. Participants were asked to attend to time from the beginning of the trial, and estimate when the stimulus was briefly presented, relative to the beginning and the end of the trial. When the trial ended, the hand of the clock was presented again, and participants used the cursor to place it at the position where it would have been at the time of the flash. On each trial, the timing of the target relative to the onset of the trial was chosen randomly. We never presented a stimulus 150 ms after the beginning or before the end of the trial. We tested 11 eccentricities (logarithmically spaced positions, from 2 to 18 dva, and a condition in which stimulus was presented centrally), in separate blocks. We presented two targets at each side of the fixation, to minimize eye movements. Before the beginning of the experiment, participants were presented with the rotating hand of the clock 15 times to memorize the fixed duration of a trial. After this familiarization phase, and after each break (10 breaks in total) participants had a short training session with feedback (30 trials at the beginning of the experiment and 10 trials after each break). In these sessions, participants completed trials with the stimulus always presented at the fixation. In the main part of the experiment no feedback was provided. Participants completed 40 trials for each distractor condition. The experiment was conducted in a single session and lasted for approximately one hour and a half.

### 5.3.2 Results

To estimate the bias of the apparent time of the target, we calculated the temporal error as a difference between reported and presented time. The average temporal error across participants is shown in Figure 5.2A. On average, participants reported stimuli earlier when they were presented in the periphery. This bias was as much as 100 ms for targets presented at 18 dva eccentricity. In Figure 4.2B, average reported time is plotted against the presented time. The presented time is binned in four equally sized bins, and for each bin and eccentricity (color coded) the bias in the reported time is averaged across participants.

We quantified the effect by means of a linear mixed-effect model. The dependent variable was the temporal error, and we modeled the fixed effect of the distractor as the second order polynomial to account for the non-linearity of the effect. We included participants as random factor to account for the additional variability. We found a significant effect of eccentricity, and both linear ( $b = -8.810^{-3}$ ,  $SE = 2.46 \cdot 10^{-3}$ ,  $t = -3.597$ ,  $p < 0.01$ ) and quadratic ( $b = 3.0210^{-4}$ ,  $SE = 1.327 \cdot 10^{-4}$ ,  $t = 2.276$ ,  $p < 0.05$ ) terms were significant. Excluding the quadratic term impaired

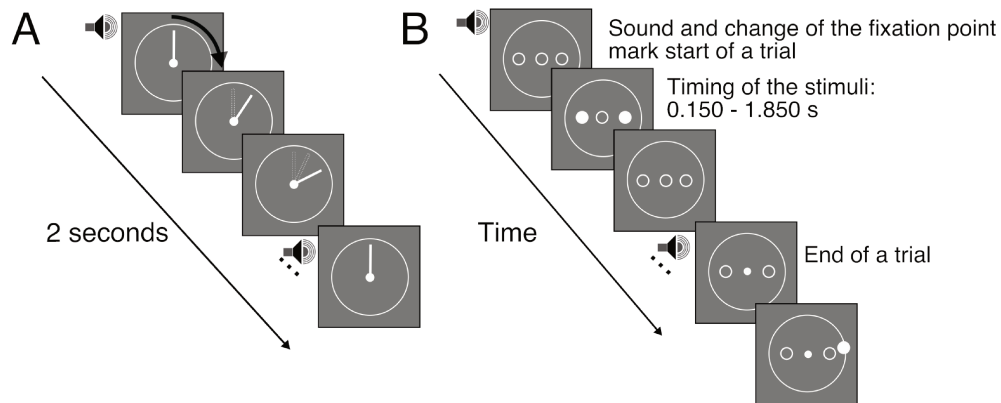


FIGURE 5.1: Representation of the temporal sequences of the familiarization phase and an experimental trial. (A). Familiarization with trial duration. At the beginning of the experiment, participants were presented with the hand of a clock rotating at a constant velocity over 2 seconds for one full revolution. A brief 1kHz pure tone was presented at the beginning and at the end of each revolution, as an additional cue to facilitate learning of the trial duration. (B). Illustration of the stimulus sequence in Experiment 1. During the experiment, the hand of the clock was removed. At the start of the trial the fixation disc changed to a placeholder for the stimulus, and a brief tone was presented. After a random delay, two stimuli at either side of fixation were simultaneously presented. The trial ended after 2 seconds. The end of the trial was marked by a change of the placeholder to a fixation disc and a brief tone. Participants moved the mouse cursor to place the hand in the position where it would have been at the time the targets were presented.

the goodness-of-fit of the model, assess by a Chi-square test ( $Chi - square(1) = 5.180, p < 0.05$ ).

## 5.4 Experiment 2

In the first experiment we showed that the apparent time of a visual stimulus is affected by its position in the visual field. Events were reported earlier when they were presented at peripheral locations. Dominant models of time perception propose that the temporal mechanism functions like a clock: units of time are pulses (*ticks*) emitted from an internal pacemaker. Perceived time corresponds to the accumulated pulses during the duration of an interval. Previous work showed that the duration between stimuli briefly presented in the periphery is compressed relative to that in the center of the visual field (Aedo-Jury & Pins, 2010; Kliegl & Huckauf, 2014). In addition, adaptation studies provided evidence for local timing mechanisms across the visual field (A. Bruno, Ayhan, & Johnston, 2011; Burr et al., 2007; Johnston et al., 2006). In particular, these studies showed that adaptation to flicker in one part of the visual field can induce local biases in perceived duration. If the local mechanisms are different across the visual field, and slower for peripheral

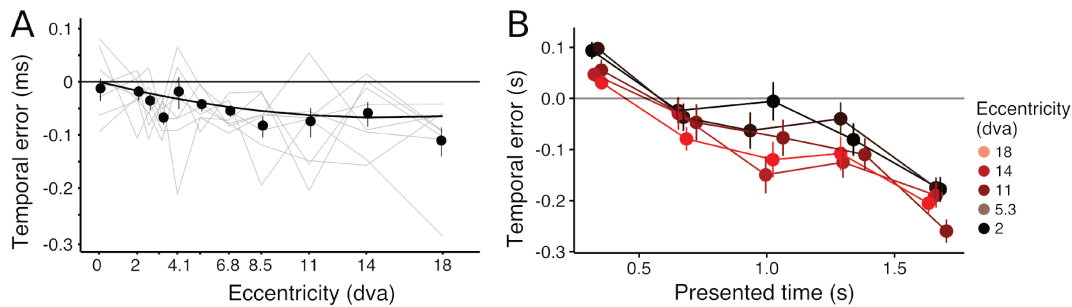


FIGURE 5.2: Results of Experiment 1. (A). Average temporal bias is shown against tested eccentricities. The bias is averaged across participants, and error bars correspond to standard error of the mean. The fit of the linear mixed effect model is shown with black line. Individual data are shown in gray lines. (B). Binned reported time against the bias for different eccentricities (color coded). There is a gradual shift in the reported time for larger eccentricities (from black to red symbols). For clarity, only five out of ten tested eccentricities are shown.

stimuli, durations in the periphery would be perceived to be shorter than durations presented in the central visual field. This explanation would predict the effect to scale with the duration of the interval. We conducted a second experiment to further test this hypothesis. In Experiment 2, participants estimated rate of a slowly flickering stimuli in a two-interval forced choice task. In the first interval, a stimulus flickering with a frequency of either 1.25 Hz or 2 Hz (*standard*) was presented. In the second interval, the rate of the flicker was varied from trial to trial (*test*), and participants were asked to estimate in which of the two intervals the stimulus flickered at a faster rate. We compared performance for two durations, which allowed us to investigate whether bias depends on the presented duration.

### 5.4.1 Method

The stimuli and apparatus were the same as in the previous experiment.

#### 5.4.1.1 Participants

Nine participants participated in the experiment. All but one of the participants (the first author) were naive to the purpose of the experiment and gave written informed consent. The experiment was conducted in agreement with the Declaration of Helsinki and the local ethics committee.

#### 5.4.1.2 Procedure

In two successive intervals, a pair of discs were presented four times, with constant interval between successive presentations. The first interval contained the stimulus

flickering at a fixed rate (*standard*), presented centrally at the fixation. In the second interval, two *test* stimuli were presented at one of the three tested locations in the visual field (2, 8.5 or 18 dva), on either side of the fixation. Participants' task was to compare the standard rate with varying test rate presented at one of the three tested eccentricities, and respond in which of the two intervals the stimulus flickered faster. The rate of the test stimulus was varied between trials, according to an adaptive staircase method. We used the adaptive stochastic accelerated staircases (Kesten, 1958; Anderson and Johnson, 2006) to find point of subjective equality (PSE) between the peripheral and foveal flicker rate. Each eccentricity was tested in a separate block. Two staircases for each of the two standards (1.25 and 2Hz) were interleaved in a block (four staircases in total).

### 5.4.2 Results

We obtained PSEs for each eccentricity and the two standard rates (1.25 and 2Hz). Averaged PSEs are plotted against tested locations in Figure 5.3, separately for the two standard rates. The two rates are color coded: gray symbols correspond to PSEs obtained for 2 Hz, and black for 1.25 Hz. The staircase for one participant did not converge, and these data were not included in the analysis. In addition to the effect of the standard rate, we found an effect of eccentricity. In particular, PSEs decreased as a function of stimulus eccentricity. In other words, to be perceived as flickering at the same rate, the frequency of flicker of the stimulus presented in the periphery should be slower than that of the foveally presented stimuli.

We quantified the effects by means of a linear-mixed model. The dependent variable was the PSE, and we included the two standard flicker rates and eccentricity as predictors. We also included participants as random factor, to account for additional variability. We found an effect of the standard rate ( $b = -0.160, SE = 0.04, t = -4.005, p < 0.01$ ), and of eccentricity ( $b = 0.006, SE = 0.002, t = 2.437, p < 0.05$ ), but no interaction between the two predictors.

### 5.4.3 Discussion of Experiments 1 and 2

In the first experiment we investigated when a visual event is perceived across the visual field. Participants estimated when a pair of white discs was presented, relative to the onset of the trial. We found that events presented in the periphery were reported earlier than those presented in the center of the visual field. In particular, the bias to report events earlier increased nonlinearly with eccentricity (Figure 5.2A). In the second experiment, we investigated the perceived rate of slowly flickering stimuli presented at different locations across the periphery. We found that

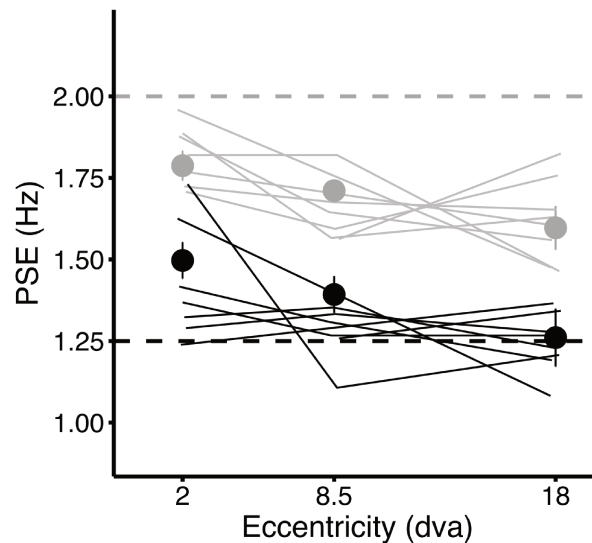


FIGURE 5.3: Results of Experiment 2. Average points of subjective equality for the two standard rates are plotted against tested eccentricities. For both standard durations, the PSEs were decreasing with the eccentricity. In other words, the rate was perceived faster (and the duration between the stimuli shorter) with greater eccentricity. There was no interaction between the two standard rates and eccentricities. Dashed lines show the value of the two standard flicker rates. Individual data are shown with lines. Error bars indicate standard errors of the mean.

the rate was perceived faster at the peripheral locations, relative to the stimulus flicker rate of centrally presented stimuli.

Our findings are at odds with a temporal order judgement study testing the relative time between centrally and peripherally presented stimuli (R. Rutschmann, 1966). More specifically, peripheral and foveal stimuli are perceived simultaneous (discrimination of temporal order at chance) when stimuli are presented earlier at the peripheral locations. These findings are interpreted as the result of different latencies across the visual field. However, in the study, the order of presentation (foveal or peripheral) was randomized. Therefore, participants did not know in advance the position of the stimulus, and the results could be confounded by the time needed to shift attention from the fixation to the peripheral stimulus.

The results of the second experiment are in agreement with previous work, showing that the perceived temporal interval between stimuli presented in the periphery is compressed relative to intervals presented in the center of the visual field (Aedo-Jury & Pins, 2010; Kliegl & Huckauf, 2014). Similarly, we found that rate is perceived faster, or the duration between the two stimuli shorter, for stimuli presented at peripheral locations. In addition, we found the same effect for the two tested standard rates, which is not consistent with the hypothesis of different clock speeds at different locations.



The failure of classical models of time to explain our effects forces us to consider alternative interpretations. Previous studies related underestimation of intervals to activity of the magnocellular pathway. For example, stimuli designed to selectively activate magnocellular pathway (luminance modulated, low spatial frequency gratings) induced time compression in the periphery, after being equalized for visibility at different locations. In contrast, color modulated, high spatial frequency stimuli did not induce this bias (Aedo-Jury & Pins, 2010). Furthermore, biases induced by adaptation to flicker or the luminance of the stimuli are also hypothesized to be related to the temporal tuning of magnocellular neurons (A. Bruno et al., 2011; Johnston et al., 2006).

Temporal properties of responses to visual stimuli are not constant across the visual field. Cells from both the magnocellular (M) and parvocellular (P) pathways of macaque monkeys are more responsive in the periphery (Solomon, Martin, White, Rüttiger, & Lee, 2002). The temporal response of the magnocellular pathway is more transient, and peaks earlier in the periphery (Solomon et al., 2002). In addition, there is an uneven mapping from the two pathways from LGN to cortex, with an exponential decrease in P:M projections ratio as a function of eccentricity (Azzopardi, Jones, & Cowey, 1999; Fukuda & Stone, 1974). In agreement with neurophysiological work on tuning of M and P cells, as well as the ratio of the two cell types, there is psychophysical evidence that the temporal impulse response in periphery is more biphasic, with a faster time course (Hess & Fredericksen, 2002; McKee & Taylor, 1984; Takeuchi & De Valois, 2009; Tyler, 1985).

In summary, there is converging evidence that different biases in time perception could be mediated by transient signals of the magnocellular pathway. Given the evidence for differences in temporal properties of responses in the periphery, in the third experiment we tested whether the bias to report events earlier in the periphery is related to the shape of the temporal response to stimuli across the periphery.

## **5.5 Experiment 3**

In Experiment 3, we tested whether the shape of the temporal response to visual stimuli is different at locations in the visual field for which we found the underestimation of the perceived time. Previous work suggests that the neural response to stimuli presented in the periphery is more biphasic, compared to the response to centrally presented stimuli (Hess & Fredericksen, 2002; McKee & Taylor, 1984; Takeuchi & De Valois, 2009; Tyler, 1985). However, to relate the two phenomena,

we tested the perceived time and the temporal response to the stimuli at those locations in the same experiment (A. Bruno et al., 2011). We used the motion reversal illusion to estimate the shape of the temporal impulse response at different eccentricities (O. J. Braddick, 1980; A. Bruno et al., 2011; Shioiri & Cavanagh, 1990; Takeuchi & De Valois, 1997, 2009). The motion reversal illusion occurs when frames presenting stimuli in motion are separated by empty frames of average luminance. For example, when two gratings with a 90 degree difference in phase are presented in succession, the strong motion percept is elicited. The presentation of blank frames with mean luminance between the two gratings affects the motion percept: the inter-stimulus interval lasting between 50 to 300 ms reverses the direction of perceived motion (O. J. Braddick, 1980; Shioiri & Cavanagh, 1990; Takeuchi & De Valois, 1997). The inter-stimulus interval for which motion reversal occurs is related to the shape of the temporal impulse response (Johnston & Clifford, 1995; Shioiri & Cavanagh, 1990). In particular, reversal in motion direction is produced by a comparison between the negative after-image produced during the period of the ISI, and the negative lobe of the impulse response and the subsequent stimulus.

### 5.5.1 Method

#### 5.5.1.1 Stimuli and Apparatus

Stimuli were vertical sinusoidal gratings, spatial frequency 2 c/deg. They were full contrast, presented on a mid gray background. Gratings were presented for 100 ms. The experiment was conducted in a dimly lit room. Experiments were created using Matlab R 2016a and Psychtoolbox-3 (Brainard, 1997; Kleiner et al., 2007). Stimuli were presented on a CRT monitor, with a resolution 1204 x 768 pixels, and refresh rate 120 Hz. The viewing distance was 30 cm.

#### 5.5.1.2 Participants

Eleven participants participated in the experiment. Three participants were male and the mean age was 24. All participants were naive to the purpose of the experiment and gave written informed consent. The experiment was conducted in agreement with the Declaration of Helsinki and local ethics committee.

#### 5.5.1.3 Procedure

Participants completed two experiments, in a counter-balanced order. The first experiment was similar to the task in Experiment 1, with a few differences: the

stimulus was a vertical grating, spatial frequency 2 c/deg, and we tested three eccentricities (fixation, at 2 and 18 dva).

In the second experiment, participants estimated the motion direction of a grating. We presented 4 gratings in succession, each with 90 deg phase shift relative to the previous one. In order to measure the motion reversal, various inter-stimulus intervals between successive gratings were presented. We tested ten logarithmically spaced inter-stimulus intervals, from 0 to 450 ms. The participant's task was to report the perceived direction of motion (drift) of the grating. The gratings were presented at three different locations in the visual field (fixation, 2 or 18 dva along the horizontal meridian). Each eccentricity was tested in a separate block.

## 5.5.2 Results

To quantify the bias in the reported time of events, we calculated the temporal error as the difference between the reported and presented times. The average temporal errors across participants for the three tested positions of the stimuli are shown in Figure 5.3A. Participants were biased to report stimuli presented in the periphery earlier, compared to stimuli presented at foveal and parafoveal locations. We quantified the effect by means of a linear mixed effect model with temporal error as the dependent variable, and eccentricity as a predictor. We included subjects as a random factor. The effect of eccentricity was significant ( $b = -3.3 \cdot 10^{-3}$ ,  $SE = 4 \cdot 10^{-3}$ ,  $t = -4.085$ ,  $p < 0.01$ ).

In Figure 5.3B, the average proportion of *leftward* responses is shown against the inter-stimulus interval between gratings. The results for the three tested eccentricities are shown in different colors. When gratings were presented at fixation (black symbols), motion was almost always detected in the same direction. Responses in this condition were probably based on feature matching, rather than a proper motion percept (Takeuchi & De Valois, 2009). For gratings presented at 2 dva (brown symbols), we found no motion reversal, but the proportion of trials for which perceived motion was in the leftward direction decreased for ISIs greater than 30 ms. Finally, when stimuli were presented in the periphery (red symbols), we found motion reversal for ISI between 30 and 100 ms.

## 5.5.3 Discussion of Experiment 3

In this experiment we tested whether the bias to report events earlier at peripheral locations coincides with different temporal responses to stimuli at those locations. In two separate experiments, we asked participants to report the time of a stimulus presented at different locations in the visual field, relative to the onset of a trial.

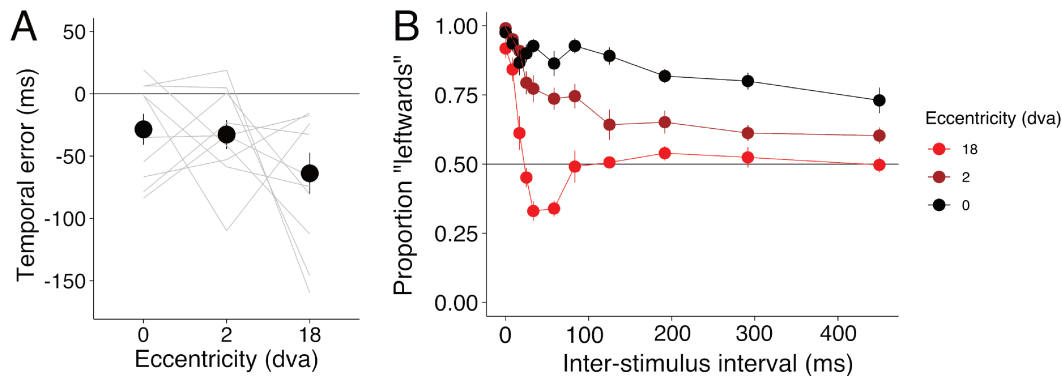


FIGURE 5.4: Results of Experiment 3. (A). Temporal error is plotted against tested locations in the visual field. Gratings presented in the periphery are reported earlier than gratings presented at foveal and parafoveal locations. Black symbols show the average across participants. Gray lines show individual data, corrected for participants' means (Loftus & Masson, 1994) (B). Results of the Motion reversal experiment. Proportion of trials in which leftwards motion was detected is plotted against the duration of the inter-stimulus intervals between gratings. Data are averages across participants. Data from different eccentricity conditions are color coded. When stimuli were presented at the fovea or 2 dva (black and brown symbols, respectively) on the horizontal meridian, no motion reversal was found. Motion reversal was found for gratings presented in periphery, for inter-stimulus intervals between 30 and 100 ms (red symbols).

Then, using the motion reversal illusion, we estimated the shape of the temporal response to stimuli at those locations. We found that stimuli were reported earlier in the periphery. In addition, motion reversal was found for at that location, suggesting a biphasic shape of the temporal impulse response (Takeuchi & De Valois, 2009; Watson, 1986).

The shape of the temporal response is different for transient and sustained systems (Watson & Nachmias, 1977). Purely sustained response has the same sign over time, and its integral is equal to the integral of the absolute value of the response. The response of a transient system, on the other hand, is biphasic, with both positive and negative lobes. The integral of the response of a purely transient system is zero, and the size of the positive and negative lobes are the same. Importantly, there is evidence that the distribution of transient and sustained responses have different distributions across the visual field (Fukuda & Stone, 1974). In addition, the sustained response has a longer time course than the transient response (Cleland, Levick, & Sanderson, 1973). In agreement with these findings, we found that motion reversal is more pronounced in the periphery. In other words, we found that stimuli presented at the locations where the response is more transient (and presumably salient), are reported earlier. The mechanisms for this bias is still not clear. Nevertheless, these findings are in an agreement with recent work showing that a disruption of transient signals biases perceived duration, simultaneity and

order (Arnold & Wilcock, 2007; Kresevic, Marinovic, Johnston, & Arnold, 2016; Morrone et al., 2005; Terao, Watanabe, Yagi, & Nishida, 2008).

The effect of eccentricity in this experiment seems to be a bit smaller than that in Experiment 1. It should be noted that in order to measure motion reversal, the stimulus was modified in a few aspects. It was presented for a longer time (100 ms instead 33 ms), which increased uncertainty about the onset and offset of the stimulus. In addition, the stimulus was a low spatial frequency grating, rather than a white disc. However, we still found an effect of eccentricity, and showed that the temporal response of the visual system was different across tested locations. The variability in temporal error as a function of eccentricity was greater between participants than that of variability in the motion reversal illusion. This difference could be partially due to different methods of the response used: for temporal estimation, a variant of the reproduction method was used, while in the motion reversal the participants chose between two alternatives. However, it is probable that temporal estimation is a more variable, higher level task, that is affected by individual biases and strategies to a greater extent. The possible confound in the motion reversal task is that different motion detection mechanisms could operate in the center and in the periphery (Takeuchi & De Valois, 2009). This is evident for stimuli presented in the fovea, where motion direction was almost perfect regardless of the temporal interval between frames. This mechanism could contribute to the pattern of the data found for stimuli presented at 2 dva. Therefore, it is important to test this hypothesis further, for example, by manipulating the transient of response systematically, at the same location in the visual field. One way to vary the response is to present stimuli with different spatial frequencies (Takeuchi & De Valois, 1997; Tappe et al., 1994; Terao et al., 2008; Watson, 1986; Watson & Nachmias, 1977).

## **5.6 General Discussion**

In the present study, we investigated the apparent time of stimuli across the visual field. In Experiment 1, events presented in the periphery were reported earlier than events presented at the fovea. In the second experiment, the rate of slowly flickering stimuli was perceived as faster in the periphery. Furthermore, we tested the hypothesis that salient transient signals are related to the underestimation of time in the periphery. We replicated the bias found in Experiment 1 with a low spatial frequency sinusoidal grating, and found that events are reported earlier at the location in the visual field where the temporal impulse response is more biphasic.

At this point, we still do not understand the mechanism underlying these effects.

The finding that the rate of slowly flickering stimuli is perceived faster in the periphery is consistent with the previous findings showing perceived duration compression in the periphery (Aedo-Jury & Pins, 2010; Kliegl & Huckauf, 2014). However, they are not consistent with the hypothesis of the timing mechanism running slower in the periphery (Kliegl & Huckauf, 2014).

The bias to report events earlier in the periphery is broadly consistent with findings that speed of processing is faster in the periphery (Carrasco et al., 2003). Intuitively, faster processing in the periphery could lead to reporting events earlier at those locations. This interpretation would imply that the perceived time of the stimulus corresponds to the time when processing is completed.

It has been proposed that the perceived time of events does not always depend on latencies (Johnston & Nishida, 2001; Nishida & Johnston, 2002, 2010; Dennett & Kinsbourne, 1994). One of the alternative hypotheses is that the perceived time of events, or *event time*, is encoded via temporal markers. Salient features from early responses are used as markers, that are compared in a mid-level processing stage (Holcombe, 2009; Johnston & Nishida, 2001; Nishida & Johnston, 2002, 2010). The effects we observed are consistent with previous work showing the importance of transient signals for the perceived time of events. For example, transients provided by an exogenous cue influence the perceived timing of features (Holcombe & Cavanagh, 2008), and modulation of transient signals biases the perception of interval duration and simultaneity (Terao et al., 2008). Furthermore, the temporal reversal of stimuli presented just before and during saccades (Binda, Cicchini, Burr, & Morrone, 2009; Kresevic et al., 2016; Morrone et al., 2005) could be explained by the reduction in the transient onset of a stimulus during the saccade, and a bias to report more transient stimuli first (Kresevic et al., 2016). Here we showed that events are reported earlier at locations for which the temporal response was more transient (Watson, 1986). Further work is needed to explain the mechanism and the origin of these biases.

One hypothesis that we have not addressed is that the bias in reported time is related to attention. For example, it has been shown that a larger spatial attention span is responsible for a lower temporal resolution (Poggel et al., 2006). In our experiment, shifting attention from fixation to peripheral locations could require a different amount of time depending on the position of the stimulus. Humans do not always take into account processing times (Duyck et al., 2015; Jonikaitis et al., 2009; Riggs et al., 1981). Therefore, if participants did not account for the duration of the shift, or overcompensate for it, perceive time would be shorter at greater

eccentricities. That said, robust findings of temporal costs of shifting attention to peripheral locations, provide evidence against this hypothesis (Carlson et al., 2006; Hogendoorn, Carlson, VanRullen, & Verstraten, 2010).

In summary, the findings reported here provide additional evidence that perceived time is not uniform across the visual field. In addition, they are in agreement with hypotheses suggesting that different signals, such as salient transients, can be used to estimate when events happened in the environment.

## 5.7 Supplementary Experiments 1A and B

In two experiments reported in this section, we explored how different parameters of the task affect the perceived time of the stimulus across the visual field. In the first experiment, stimuli and the procedure were identical to that in Experiment 1. The difference was in the meridian along which we tested the effect of the eccentricity: in this experiment the stimuli were presented along the vertical meridian. Results for the four participants are shown in Figure 5.4A. In the second experiment, we tested whether change in contrast polarity (from black to white), of targets that were present throughout the trial will also be underestimated for the stimuli presented in the periphery. As shown on Figure 5.4B, changes in the contrast of the stimuli were also reported earlier for the stimuli presented at the peripheral locations, relative to those presented centrally.

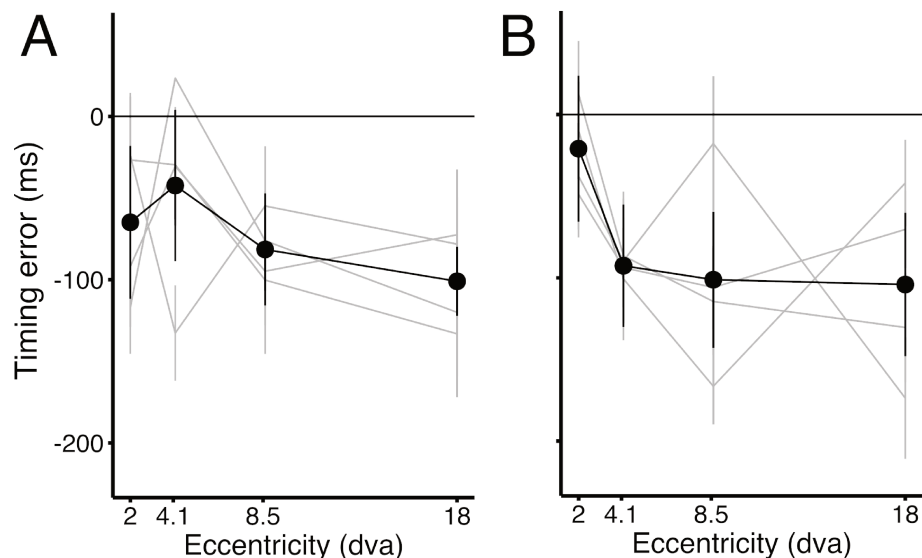


FIGURE 5.5: Temporal bias for stimuli presented on the vertical meridian (A) and for change of contrast (black to white) (B). Average temporal bias is shown against tested eccentricities. The bias is averaged across participants, and error bars correspond to standard errors of the mean. Individual data with corresponding standard errors are shown in gray lines.

## 5.8 Supplementary Experiment 2

In the experiment reported here, we tested whether the change in the size of cortical representation of stimuli presented at different positions in the visual field is responsible for the bias to report the events earlier in the periphery. The stimuli, apparatus and procedure were the same as in Experiment 1, and we tested six participants. The difference was in the stimuli size: in this experiment, the size of the



stimuli was scaled to match the size of the cortical representation in V1 (Duncan & Boynton, 2003). In addition, the size of the hand of the clock was 9 dva (instead of 2.5 dva in Experiment 1 and 3). As shown on Figure 5.5, the stimuli presented at greater eccentricities were reported earlier.

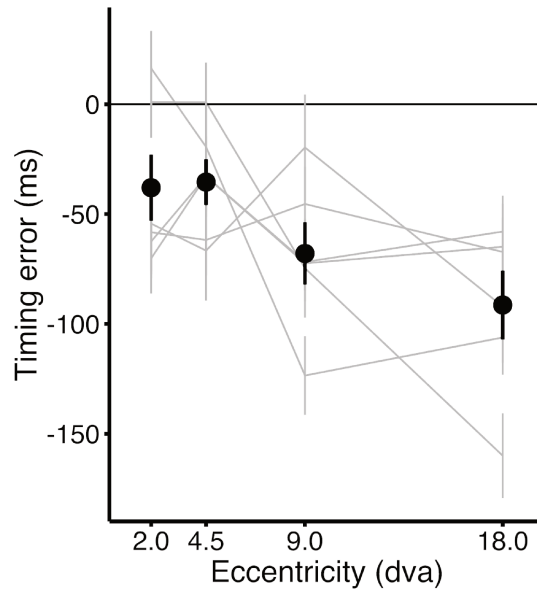


FIGURE 5.6: Temporal bias with M-scaled stimuli (Duncan & Boynton, 2003). In this experiment, the size of the stimuli was scaled to match the size of the cortical representation in V1. The hand of the clock in this experiment was 9 dva, instead of 2.5 as in Experiments 1 and 3. Average temporal bias is shown against tested eccentricities. The bias is averaged across participants, and error bars correspond to standard errors of the mean. Individual data with corresponding standard errors are shown in gray lines. Black symbols represent the mean bias across participants (with corresponding standard errors), and gray lines are individual data (error bars are standard error of the median).

## 5.9 Supplementary Experiment 3

In this experiment we investigated whether the perceived rate of flickering stimuli depends on the spatial frequency of the stimuli. The temporal response of the visual system depends on the stimulus spatial frequency (Takeuchi & De Valois, 1997; Watson & Nachmias, 1977), and the response to high spatial frequency stimuli is monophasic for high spatial frequencies. If the shape of the temporal impulse response is related to the underestimation of perceived duration, the flicker of stimuli with low spatial frequencies should be perceived as flickering faster (duration between stimuli perceived shorter), than that of high spatial frequency stimuli.

### 5.9.1 Method

#### 5.9.1.1 Stimuli and Apparatus

Stimuli were sinusoidal gratings, size 2 dva, spatial frequency 1, 3 and 8 c/deg. The three values of the spatial frequency were chosen based on the pilot motion reversal experiment. Stimuli were full contrast, and presented on a black background at a refresh rate of 120 Hz. The viewing distance was 60 cm.

#### 5.9.1.2 Participants

Eight participants participated in the experiment. Three participants were male and the mean age was 25. All participants, except for the first author were naive to the purpose of the experiment and gave written informed consent. The experiment was conducted in agreement with the Declaration of Helsinki and the local ethics committee.

#### 5.9.1.3 Procedure

As in Experiment 2, participants were presented with slowly flickering stimuli. The task was to compare two flicker rates presented successively in two intervals. In the first interval, the standard rate (1.25 or 2Hz) was presented, and stimuli were mid-gray squares, size 2 dva. In the second interval, the rate of the flicker was varied from trial to trial, according to the adaptive stochastic accelerated staircase procedure, in order to reach the point of subjective equality. Stimuli in the second interval were vertical sinusoidal gratings. We tested three spatial frequencies (1, 3 and 8 c/deg). Each spatial frequency was tested in a separate block. In one block, two staircases for each of the standard rates were interleaved (4 staircases in total).

## 5.9.2 Results

Staircases for one participant did not converge and data were not included in the analysis.

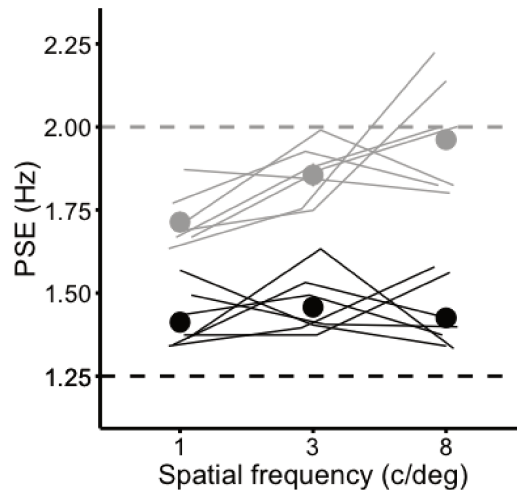


FIGURE 5.7: Results of the supplementary experiment. Average points of subjective equality for the two standard rates are plotted against tested spatial frequencies.

We quantified the effects by means of a linear-mixed effects model. We included participants as random factor, to account for additional variability. We found an effect of standard rate ( $b = -0.113$ ,  $SE = 0.03$ ,  $t = -3.9$ ,  $p < 0.01$ ), but no effect of spatial frequency or their interaction.

In this experiment, participants estimated the rate of slowly flickering stimuli of varying spatial frequency. The difference between temporal response to low and high spatial frequencies is similar to that between the central and peripheral visual field. Therefore, we asked whether the difference between the perceived rate of stimuli with low and high spatial frequency will be similar to that between the periphery and fovea. Consistent with this hypothesis, we found that the rate of flicker of low spatial frequency stimuli was perceived faster (and intervals between stimuli shorter), relative to rate the of high spatial frequency stimuli. Nevertheless, this was true only for the faster of the two flicker rates.

## 5.10 Conclusions

In this chapter I presented a series of experiments that addressed the question of whether perceived time of visual events depends on the position in the visual field. In addition, the study was inspired by a fundamental question, regarding which information about the stimuli is relevant for estimating when an event was presented. A bias to report events presented in the periphery earlier is reported. The perceived time of events as assessed in this task is not in agreement with latency differences found in temporal order judgement task. At this point, it is not clear what causes the effects. They are broadly consistent with the findings about the different processing speed across the visual field, and the hypothesis that saliency of events may be relevant cue for encoding time of events. Future work should further address these hypotheses.



## When an event is perceived depends on where we attend

Here I present two experiments that preceded the work presented in the Chapter 6, in which I explored how spatial features of the display affect the reported time of visual events in the *clock* task employed in Chapters 4 and 5. For instance, it has been shown that in the task in which participants were asked to estimate when external stimuli were presented relative to a rotating hand of a clock was affected by the stimulus modality and the speed of the hand rotation (Danquah, Farrell, & O'Boyle, 2008). I report here that spatial proximity to salient spatial features of the display, even when not displayed during the trial, strongly bias the reported time of the visual events.

## 5.11 Introduction

Humans can distribute attention to multiple locations in space (Cheng et al., 2014; McMains & Somers, 2005; Pylyshyn & Storm, 1988; Scholl, Pylyshyn, & Feldman, 2001). When attention is divided between the duration of a stimulus and other features of the stimulus, the perceived duration of the stimulus is reduced, suggesting that the processing of the duration of a stimulus shares the same, limited attentional resources as the processing of other features of that stimulus (Block & Gruber, 2014; Block & Zakay, 1997; Coull et al., 2004; Klapproth, 2011; Macar, Grondin, & Casini, 1994; Tse, Intriligator, Rivest, & Cavanagh, 2004; Zakay & Block, 2004). For example, when participants are explicitly asked to attend to the duration of a word and the word meaning to a different extent, their estimates of the duration scale positively with attention allocated to the stimulus duration (Macar et al., 1994). In contrast, when the stimulus captures attention, its duration is overestimated (Tse et al., 2004). Both sustained and transient attention can impair temporal resolution. Discrimination thresholds for two successive visual pulses are higher when transient attention is directed to their spatial location (Yeshurun & Levy, 2003), or when the attentional focus is diffused across a large area (Poggel et al., 2006). When attention is divided across different, spatially disparate, durations, spatial uncertainty decreases the precision of duration judgements (Ayhan et al., 2012). Similarly, a visual search task showed that the search for a temporal oddball deteriorated very quickly with increased set size (Morgan, Giora, & Solomon, 2008).

These findings suggest that time perception shares resources with other cognitive processes (Macar et al., 1994), that the timing of multiple intervals is demanding, and that humans have difficulty in simultaneous timing (Ayhan et al., 2012; Morgan et al., 2008). Here we report that when an event is perceived depends on where it is presented relative to the attended spatial location. In our task, participants attended the passage of time, while simultaneously monitoring locations in the visual field where the stimulus appeared. At the beginning of the experiment, they were presented with a fixed duration of one trial, by watching the hand of the clock rotating at a constant velocity. In the main part of the experiment, the hand of the clock was removed, and participants were asked to attend to the time from the onset of the trial. The onset and the offset of the trial were indicated by changes of the fixation and a brief sound. A white disc was flashed briefly at different locations on the horizontal meridian. At the end of the trial, participants gave the response by moving the cursor to indicate where the hand of the clock would have been at the time of the flash.

To investigate whether the reported time of visual events depended on the position of the event relative to the salient spatial features of the clock, we varied appearance of the spatial features in two experiments. We varied the size of the clock hand, so that the tip of the hand was in spatial proximity of different tested locations. Furthermore, the spatial features presented during the trial were different in the two experiments. In Experiment 1, the outline of the clock and the stimulus outline were presented during the trial. In Experiment 2 they were not presented, and only the fixation point was presented for the full duration of the trial.

## 5.12 Method

### 5.12.1 Stimuli and apparatus

The stimulus was a white disc with a radius of 2 dva, flashed briefly (33 ms) at different positions on the screen. The background was mid-gray, and fixation point was a white disc, of size 1 dva, that changed luminance to dark gray as a preparation signal, just before the beginning of the trial. The hand of the clock had radius of 5 dva (Experiment 1) or 9 dva (Experiment 2), and it was also white. In Experiment 1 a white circle, representing the face of the clock was presented during the familiarization phase, and remained on the screen throughout the experiment. Each trial started and ended with a 33 ms pure tone, frequency 1 kHz.

The experiment was conducted in a dimly lit room. Experiments were created using Matlab R 2016a and Psychtoolbox-3 (Brainard, 1997; Kleiner et al., 2007). Stimuli were presented on a LCD flat screen (ViewSonic V3F245), with diagonal 24 in, resolution 1920 × 1080 pixels, and refresh rate 60 Hz. The viewing distance was 30 cm. The analysis of the data was conducted in the R Studio environment, using packages *lme4* (Bates et al., 2018) and *multcomp* (Hothorn et al., 2017) for mixed effect regression analysis. We excluded trials with an error larger than 120 degrees from analyses (less than 5% of the trials were excluded).

### 5.12.2 Participants

Eleven participants took part in the two experiments. All but one of the participants (the author, who took part in both experiments) were naive to the purpose of the experiment and gave written informed consent. The experiments were conducted in agreement with the Declaration of Helsinki and the local ethics committee.



### 5.12.3 Procedure

At the beginning of the experiment, participants were familiarized with a fixed trial duration by watching the hand of a clock rotating at a constant speed, one cycle in 2 seconds. To provide an additional cue for remembering the duration of the trial, a brief tone (33 ms, 1 kHz) was presented at the beginning and the end of each revolution. During the main experiment, the hand of the clock was no longer presented, and participants were asked to fixate at the center of the screen during the trial. At the beginning and the end of the trial, two brief tones were presented. A stimulus was flashed at a random time between the beginning and the end of the trial. To minimize attentional redirection to one hemifield, two stimuli were simultaneously presented on either side of fixation. Participants were asked to attend to the time from the beginning of the trial, and estimate when the stimulus was briefly presented, relative to the beginning and the end of the trial. When the trial ended, participants used the cursor to place it at the position where the hand of the clock would have been at the time of the flash. On each trial, the timing of the target relative to the onset of the trial was chosen randomly. The stimulus was never presented 150 ms after the beginning or before the end of the trial. In five blocks stimuli were presented at different locations in the visual field.

In Experiment 1 the size of the hand of the clock was 5 dva. We tested five logarithmically equally spaced positions in the visual field, from 0 to 36 dva. During the exposure phase and the trial, the outline of the clock and stimuli were presented (Figure 1A and upper panel of Figure 2). In Experiment 2 the size of the hand was 9 dva, and stimuli were presented at the same five eccentricities. We also minimized the spatial features of the clock, by removing the clock outline and stimulus placeholders both from the exposure and the test phase (lower panel of Figure 2). We also changed the response probe, and instead of placing the cursor on the outline of the clock, hand of the clock reappeared, and participants adjusted the angle to match the perceived time, by moving the cursor. An illustration of the stimuli in the two experiments is shown in Figure 2. Importantly, there was no uncertainty about spatial locations of the stimuli, as the location of the stimulus was always the same within one block. In addition, the location of the features of the clock were not predictive of the stimulus location. Before the start of the experiment and after each break, participants were presented with a rotating hand of the clock 15 times to help them memorize the duration of the trial, and then had a short training session with feedback. In the main part of the experiment no feedback was provided. Participants completed 40 trials for each distractor condition. In Experiment 1 participants completed 50 trial, and in Experiment 2, 40 trials in each condition. Each experiment was conducted in a single session, and each lasted for approximately

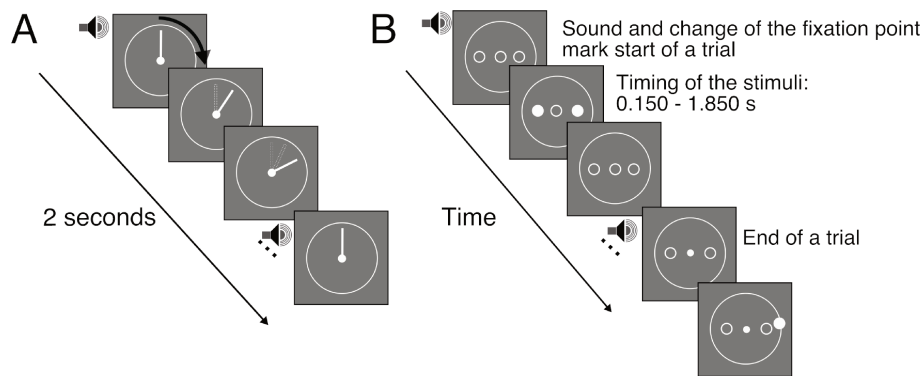


FIGURE 5.8: Representation of the temporal sequences of the familiarization phase and an experimental trial. (A). Familiarization with trial duration. At the beginning of the experiments, participants were presented with a clock. The hand of the clock rotated at a constant velocity, 2 seconds per revolution. A brief 1 kHz pure tone was presented at the beginning and at the end of each revolution, as an additional cue to facilitate learning of the trial duration. (B). Illustration of the stimulus sequence in Experiment 1. During the experiment, the hand of the clock was removed and the white circle representing the face of the clock remained on the screen. At the start of the trial, the fixation disc changed to a placeholder for the stimulus, and a brief tone was presented. After a random delay, two stimuli at either side of fixation were simultaneously presented. The trial ended after 2 seconds. The end of the trial was marked by a change of the placeholder to the fixation disc and a brief tone. Participants moved the mouse cursor to place it on the clock face at the location where the hand of the clock would have been at the time of the targets presentation. The procedure was similar in the Experiment 2, but the spatial features of the clock were reduced, and the response probe was changed. For details, see Figure 2.

one hour.

## 5.13 Results

To assess whether the moment when an event is perceived depends on the location in the visual field where it was presented, we calculated the temporal error as a difference between the presented and reported time. On Figure 3 the average temporal errors across participants are plotted against the tested positions in the visual field. Negative temporal errors indicate that the target was reported earlier than it was presented. We found a large negative bias for eccentricities that were close to the tip of the hand of the clock. Importantly, the bias was different for the two experiments. In particular, the bias shifted to larger eccentricities as the length of the hand was extended (Figures 3A and B). Additionally, there was an effect of eccentricity; stimuli presented further in the periphery were reported earlier.

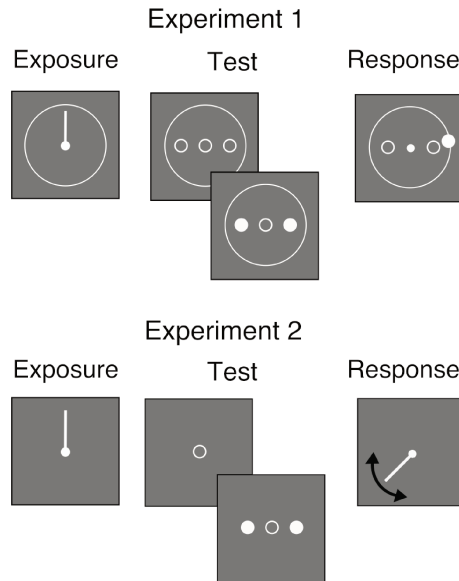


FIGURE 5.9: Stimuli presented in Experiment 1 (A) and Experiment 2 (B). (A) In Experiment 1, during the exposure phase, the hand of the clock and clock face were presented. In the test phase, the clock face and an outline of the stimuli were presented during the trial. Stimuli were briefly presented at the location of the stimulus outline, and participants estimated when the stimuli were presented, relative to the onset of the trial. The response was given by placing the cursor on the clock face, at the location where the hand of the clock would have been at the time of the stimulus. (B) In Experiment 2, the spatial features of the clock were reduced, and the response probe was changed. In the exposure phase, only a rotating hand of the clock was presented. During the test phase, only the fixation point was presented, except when the stimuli were briefly shown. The response was given by rotating the hand of the clock, to indicate the time from the beginning of the trial when the target was shown. The hand length was 9 dva (instead of 5 dva in Experiment 1).

We quantified the effect in the two experiments by means of two linear mixed-effect models. The temporal error was the dependent variable, and the tested locations in the visual field were included as a fixed factor. We also included participants as a random effect (intercept only), to account for additional variability. We tested whether the temporal errors were different for each eccentricity level, relative to the centrally presented stimuli, and corrected the significance level for simultaneous inference, using Bonferroni correction (Hothorn et al., 2017). In Experiment 1, we found an effect of eccentricity ( $F(4,1411) = 10.704, p < 0.01$ ). The contrasts revealed that the targets presented at all tested locations in the visual field were reported earlier than the targets presented at the fovea. In Experiment 2, the effect of eccentricity was also significant ( $F(4,1411) = 8.53, p < 0.01$ ). The targets presented at each peripheral location were reported earlier than the targets presented at the center of the visual field.

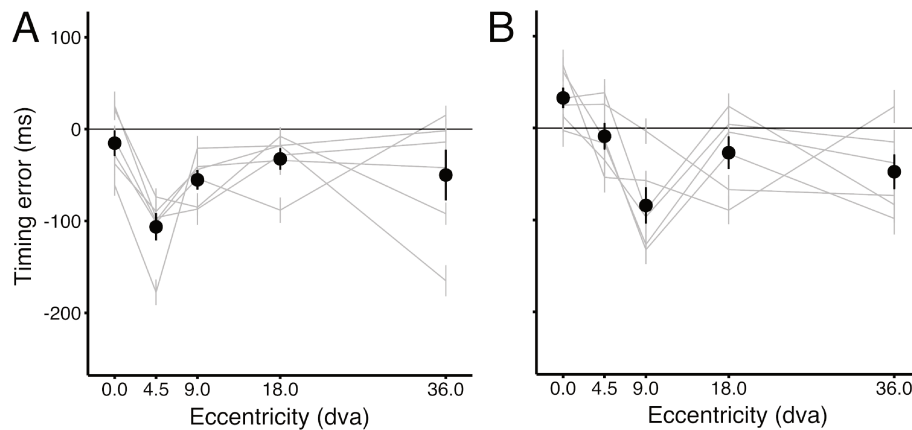


FIGURE 5.10: Results of Experiments 1 and 2. (A). The mean temporal errors in Experiment 1 are plotted against the tested locations. Negative errors indicate that the target was reported earlier than presented. The targets are reported earlier if they are presented close to the spatial features of the clock. In addition, the targets are reported earlier if they are presented further in the periphery. (B). The average temporal errors plotted against the different peripheral locations tested in Experiment 2. As in the previous experiment, when targets are presented near the spatial features of the clock, they are reported earlier. Importantly, the bias shifted compared to Experiment 1, since the tip hand of the clock was close to 9 dva. The targets are in general reported earlier if they are presented at greater eccentricities. Error bars represent standard error of the mean.

## 5.14 Discussion

In the work reported here, we asked when an event is perceived when it is presented at different locations in the visual field. We adapted the procedure previously used to investigate the perceived time of decisions (Libet et al., 1983). Participants were first familiarized with a fixed duration of the trial, by watching the hand of the clock rotating at a constant velocity. In the main experiment, the hand of a clock was no longer presented, and participants were asked to attend to the time relative to the start of the trial. We asked participants to estimate where the hand of the clock would have been at the moment when the stimulus was presented, relative to the onset of the trial. In two experiments, we varied the spatial features of the clock (the size of the hand of the clock and the presence of the clock and stimulus outline). We found that the targets were reported earlier if they were presented in spatial proximity to the spatial features of the clock. The bias was found in both experiments, even though in Experiment 2 no spatial features were presented during the trial. Importantly, the position in the visual field where the effect was found depended on the position of the spatial features. In order to perform the task, participants mentally attended to the positions of the clock's hand during the trial. During this tracking, attention could be allocated to the spatial locations of the hand of the clock in the exposure phase. There are different possible

interpretations of the observed bias. First, events that were presented close to the attended location could be perceived earlier. This hypothesis is in an agreement with previous work showing that attended targets are perceived earlier, and that attention can speed up processing at attended locations in space (Carrasco et al., 2004, 2003; Spence & Driver, 2004). Alternatively, adaptation studies provide evidence for the existence of local clocks across the visual field, whose speeds can be selectively changed by adaptation (Johnston et al., 2006). In agreement with this hypothesis, targets presented at different eccentricities are processed by these localized mechanisms. Sharing attention at a particular spatial location, by allocating the central time-keeping mechanism that is shared across the eccentricities and the local clock at the same location, could cause slowing down of the timing mechanism at that location (Block & Zakay, 1997; Zakay & Block, 2004). In summary, we found that when the attention is endogenously allocated to specific spatial coordinates, the reported time of an event is affected by its position relative to that attended location. These results are consistent with previous work indicating a limited attentional resource for time estimation (Ayhan et al., 2012; Morgan et al., 2008; van Rijn & Taatgen, 2008). Our findings support the hypothesis of a single shared resource that is employed to compare the perceived time of an event at one location, and the time elapsed from the beginning of the trial. It is an open question whether this mechanism is part of the dedicated temporal processing mechanism, or it is operating at another, possibly higher, level of cognitive processing.

## 5.15 Conclusions of Part II

In Part 2 of this thesis I investigated how the perceived time of single, brief, auditory or visual events is affected by their temporal and spatial context. In agreement with the work discussed in the introductory chapter, the findings suggest that the perceived time cannot be separated from the immediate temporal or spatial context. In the experiment in which we changed the duration/speed of the hand of the clock we obtained modified results. These findings indicate that certain task- and experiment-irrelevant, spatial and temporal characteristics can affect results in a systematic way. Therefore, the interpretation of the results should take these caveats into account. On the other hand, these biases are interesting by themselves, since they provide additional evidence of the malleability of perceived time. These findings contribute to great body of work suggesting that perceived time of events is at least partially determined by their context, which is something models of temporal processing should be able to account for.



## **Part III**

### **Timing and self-evaluating the action**









## Chapter 6

# Timing an action and being confident about it

In the previous chapters I presented work investigating the perceived time and duration of visual and auditory events. However, motor responses were required in the tasks used in these studies, and motor variability certainly contributed to the performance. The motor performance was not in the focus of studies, and therefore its variability was treated as noise rather than a variable of interest. Nevertheless, it is important to understand these motor contributions to timing behavior. Studies addressing the optimality of temporal sensorimotor performance suggest that humans might have more difficulty in performing optimally in temporal, than in spatial tasks (Hudson, Maloney, & Landy, 2008; Jarvstad, Hahn, Warren, & Rush-ton, 2014; Mamassian, 2008; Wu, Dal Martello, & Maloney, 2009). On the other hand, research exploring the metacognitive inference in the context of time perception is scarce. Here I present a project that explored the anticipated time of events in the context of an action. In particular, it was investigated how the action is timed and self-evaluated, as a function of various sources of temporal uncertainty. The question was addressed in two ways: analyzing how reaction time and movement duration change with the task requirements, and by analyzing their relationship and the explicit self-evaluation about the performance.

## 6.1 Abstract

We investigated how humans time an action, and how well they can evaluate its outcome when synchronizing an arm movement with predictable visual stimuli. On each trial, participants had to decide when to start (reaction time) and for how long to move (movement duration) to reach the target on time. After each trial, participants also estimated their confidence that their movement was timed correctly. In different conditions, we varied sensory and motor noise. To properly time their movement, we found that participants mostly varied their reaction time, keeping the average movement duration short and relatively constant across conditions. Interestingly, confidence judgments were predicted by absolute deviations in reaction time, but not movement duration. These results indicate that humans control the timing of their actions primarily by adjusting when they initiate their movement, and their metacognitive assessment of their timed action relies on the precision of this movement initiation.

## 6.2 Introduction

Movement planning and execution are under-constrained problems. For example, a simple reaching movement can be accomplished with an infinite number of trajectories and durations (Engelbrecht, 2001). However, humans plan and execute actions in a manner that maximizes their gain in different visuo-motor tasks. More specifically, humans take into account their sensory and motor uncertainty (Battaglia & Schrater, 2007; Faisal & Wolpert, 2009) as well as biomechanical costs (Cos, Belanger, & Cisek, 2011; Cos, Duque, & Cisek, 2014; Cos, Medleg, & Cisek, 2012; Soechting & Lacquaniti, 1981). Moreover, they integrate information about uncertainty with externally imposed gains in space (Dean, Wu, & Maloney, 2007; Trommershäuser, Maloney, & Landy, 2003) and time (Hudson et al., 2008), resulting in optimal movement execution that maximizes the gain in a specific context.

However, movement execution is not always optimal (Jarvstad et al., 2014; Maloney & Zhang, 2010; Mamassian, 2008; Wang, Xiao, Burdet, Gordon, & Schweighofer, 2016; Wu, Trommershäuser, Maloney, & Landy, 2006; Zhang, Wu, & Maloney, 2010). For example, when asked to allocate fixed time to two targets, humans perform sub-optimally and show consistent biases (Wu et al., 2009). Similarly, in an anticipatory motor task, participants were asked to estimate when the last stimulus, in a sequence of three, would appear and press a key to synchronize their keypress with the timing of that stimulus (Mamassian, 2008). Participants were

overconfident in their performance and/or underestimated value of rewards, and did not adjust optimally hitting time to account for variability of their action.

Estimating the correctness of one's own perceptual or motor decisions can give us some insights on the reasons why decisions are more or less precise. In perception, studies of confidence have provided good evidence that humans are able to reliably estimate the accuracy of their own performance (Barthelmé & Mamassian, 2010; de Gardelle & Mamassian, 2014; Yeung & Summerfield, 2012). Furthermore, metacognitive judgements on a sensory task are also informed by the motor system, and disrupting response motor representations in premotor cortex selectively disrupted confidence judgements (Fleming et al., 2015). Judging confidence about performed actions has been far less researched. It has been shown that humans are able to estimate both direction and degree of their temporal errors in a simple temporal reproduction task (Akdoğan & Balci, 2017; Kononowicz, Roger, & van Wassenhove, 2017). However, it seems that task complexity can affect metacognitive judgement, given that metacognitive performance was worse in blocks where more than one duration was presented (Akdoğan & Balci, 2017; Kononowicz et al., 2017).

In the work presented here, we investigated how humans time an action when asked to synchronize their arm movement with temporally predictable visual stimuli. We asked two questions. First, we investigated how participants trade off reaction time and movement duration in relation to different sources of uncertainty. On each trial, participants had to estimate the interval between the first two stimuli and then decide when to start (reaction time) and for how long to move (movement duration) to reach the target on time. We manipulated target size and orientation to affect the movement duration needed to perform the task correctly. More specifically, smaller targets require higher spatial precision and longer movement duration (Fitts, 1954). This manipulation allowed us to investigate whether timing an action is sensitive to, and compensates for temporal requirements of movement execution related to spatial difficulty. Furthermore, we varied duration of the interval between the first two stimuli. Since the shorter intervals are encoded with less noise (Gibbon, 1977; Jazayeri & Shadlen, 2010), we investigated whether the trade off is affected by different stimulus uncertainty.

The second question we asked is whether humans can estimate accuracy of their own actions, and whether accuracy and confidence in actions are affected by the same factors. Although there is evidence that humans can monitor their temporal reproduction errors well (Akdoğan & Balci, 2017), it is not clear whether temporal motor variability is always estimated correctly (Hudson et al., 2008; Mamassian, 2008). Perception of time and its reproduction rely on different brain structures

(Buetti, Walsh, Frith, & Rees, 2008) and thus performance and confidence can be disrupted independently (Fleming et al., 2015; Rahnev, Maniscalco, Luber, Lau, & Lisanby, 2012). Here we ask participants to perform a sensori-motor task that allows us to disentangle the two components of their performance: reaction time and movement duration. Therefore, movement execution will have a larger contribution to the performance compared to the key press used in previous studies. While both reaction time and movement duration will inevitably affect performance, it is an open question whether confidence about performance depends on both components of the movement equally. For example, there is an attenuation of sensory signals when the outcome of an action is predictable (Blakemore, Wolpert, & Frith, 2000; Cardoso-Leite, Mamassian, Schütz-Bosbach, & Waszak, 2010; Wolpert, 1997). Sensory attenuation could affect our ability to evaluate the outcome of our motor actions by reducing sensory cues on the movement. Also, changes in motor cortical excitability due to TMS pulses to motor cortex affect the onset, but not the offset of the movement, suggesting different and possibly subcortical mechanisms for movement offsets (MacKinnon & Rothwell, 2000). If confidence is informed solely by cortical mechanisms (Kepecs, Uchida, Zariwala, & Mainen, 2008; Kiani & Shadlen, 2009), it will have limited or indirect access to movement offset, and the two components of the action would have different weights on the evaluation of the outcome.

## 6.3 Method

### 6.3.1 Participants

Ten human participants (5 male, two left handed, mean age 24.8) took part in the experiment after giving their informed consent. All participants had normal or corrected to normal vision. Sample size was determined based on the previous studies (Barthelmé & Mamassian, 2010; Mamassian, 2008; Trommershäuser et al., 2003). The study was conducted at University of Barcelona and was part of a program that was approved by the University of Barcelona's ethical committee.

### 6.3.2 Apparatus

Participants sat in front of a drawing tablet (Calcomp DrawingTablet III 24240) that recorded movements of a hand-held stylus. Stimuli were projected from above by a Mitsubishi SD220U ceiling projector onto a horizontal back-projection screen positioned 40 cm above the tablet. Images were projected at a frame rate of 85 Hz

and a resolution of 1024 by 768 pixels (61 × 45 cm). A half-silvered mirror midway between the back-projection screen and the tablet reflected the images shown on the visual display giving participants the illusion that the display was in the same plane as the tablet. Lights between the mirror and the tablet allowed participants to see the stylus in their hand. A custom program written in C and based on OpenGL controlled the presentation of the stimuli and registered the position of the stylus at 125 Hz. The software ran on a Macintosh Pro 2.6 GHz Quad-Core computer. The set-up was calibrated by aligning the position of the stylus with dots appearing on the screen, enabling us to present visual stimuli at any desired position of the tablet.

### 6.3.3 Data analysis

The analysis of the data was conducted in R Studio environment, using packages *lme4* (Bates et al., 2018) and *car* package (Fox et al., 2007) for mixed effect regression analysis. Position data were smoothed with Butterworth filter (cut-off at 8 Hz). We cleaned the data by removing trials that had extreme reaction times (larger than 2.5s) and movement duration (larger than 2s). Less than 5% of the data were excluded from the analysis.

### 6.3.4 Stimuli

Stimuli were three white ellipses presented on the horizontal plane on a black background. The center of the ellipse was located at 25 cm from home position. We systematically varied size, orientation, and temporal interval between sequential presentation of the stimuli. The length of major and minor axes of ellipses were varied in 4 equal linear steps, from 0.8 to 3.2 and 0.4 to 1.6 cm, respectively. We tested two orientations, with the major axis being either perpendicular or in the line with arm movement (as the example shown in Figure 6.1). In the rest of the report, we refer to these two orientations as horizontal and vertical, respectively. The temporal intervals were varied in 5 logarithmically equally spaced steps, from 0.8 to 1.8 seconds (0.8, 1, 1.2, 1.5 and 1.8 seconds).

### 6.3.5 Procedure

Participants were asked to synchronize the end of their hand movements with a temporally predictable visual stimulus presented on a horizontal plane. After the consecutive presentation of two stimuli, participants moved their dominant hand



in order to point to a target third stimulus. The timing of the target could be inferred from the interval delay between the two first stimuli. In other words, participants had to estimate the duration between the first and the second stimulus presentations. Then, they had to plan and execute the movement so as to reach the third stimulus at the moment this stimulus was presented. They could anticipate that time because the duration between the first two stimuli equaled the duration between the second stimulus and the third. Each trial started with participants placing their hand holding a pen at the initial position (see Figure 6.1) and outlines of three ellipses of the same size and orientation were presented. First the leftmost and then the middle ellipse turned white. Participants were asked to synchronize their movement with the predictable sequence given by interval between the first two ellipses, and to arrive at the target third ellipse at the time would have turned white. The target ellipse never actually became white, so no temporal feedback was provided during the experiment. After each set of 50 trials, participants were informed about their cumulative performance on the set. For the two left-handed participants the display was reversed, so that they could perform the experiment with the dominant hand. For each trial, after the movement was executed, participants estimated their confidence about their performance for that trial. They had to estimate both their spatial and temporal accuracy, namely whether the landing position of the pen was inside the target and whether it was at the expected presentation time. While the spatial performance was trivial to estimate given that the outline of the target was visible, their temporal performance was the critical aspect of their confidence judgment. Participants were asked to provide a binary confidence estimate, by answering whether on that trial their performance was better or worse than the average performance on all previous trials. Before beginning the experimental session, participants completed 80 training trials with feedback. Participants either heard a tone if they performed correctly (reached the target within  $\pm 15\%$  of the target interval), or otherwise saw a horizontal bar of a length that corresponded to the magnitude and direction of temporal error (if the bar was on the left from the target participant reach the target too early, and if on the right participant was too late).

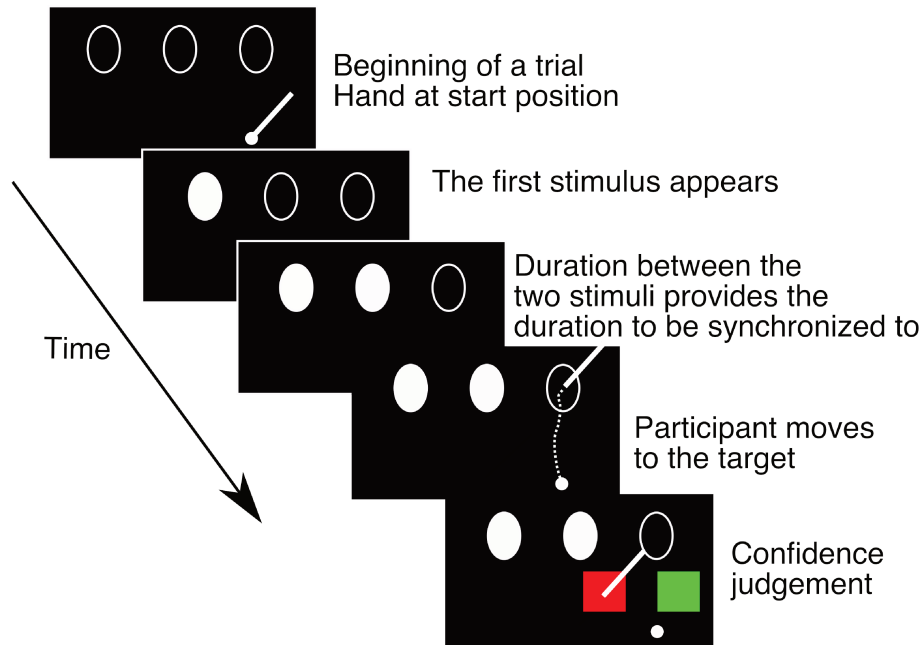


FIGURE 6.1: Schematic representation of one trial (view from above). A trial starts when the participant's hand is at the starting position, and the three stimuli outlines are presented on a horizontal plane. The temporal sequence to be synchronized to is provided by the temporal interval between the first two stimuli. After movement execution, two squares (green and red) are presented below the target. Participants estimate the confidence in the accuracy of their performance by placing their hand within the red (performance worse than average) or green square (performance better than average).

## 6.4 Results

### 6.4.1 Spatial accuracy is affected by size and orientation of the target

We quantified performance on the spatial aspect of the task by calculating the proportion of the trials for which participants ended their movement inside the target stimuli (spatial hit), separately for each condition. Hitting accuracy was affected by the size of the target and orientation, but not by the duration of the interval participants were synchronizing to (Figure 6.2A). To quantify this effect, we fitted the data with a generalized linear mixed effect model. The logarithm of presented duration, the target size, and its orientation were within-subject fixed effects. Interval duration and size were continuous variables, and orientation was treated as a factor with two levels. We also included the interaction between size and orientation. The dependent variable was hit/miss on a given trial and the random structure consisted of a random intercept and a slope for size for each subject to account for additional variability. We observed a significant effect of target size

(Wald Chi-square (1) = 143.52,  $p < 0.01$ ) and orientation (Wald Chi-square (1) = 58.71,  $p < 0.01$ ). Participants were more likely to perform correctly if the target was larger (slope = 3.96 rate of change of odds for answering correctly with increments of size  $\exp(3.96) = 52.457$ ,  $SE = 0.33$ ,  $p < 0.01$ ). Odds for correct response for vertical target were 0.543 smaller than odds for horizontal target ( $b = -0.61$  ( $\exp(b) = 0.543$ ),  $SE = 0.08$ ,  $p < 0.01$ ). The interaction between size and orientation was marginally significant (Wald Chi-square (1) = 3.491,  $p = 0.062$ ), and there was no effect of temporal interval (Wald Chi-square (1) = 0.89,  $p = 0.345$ ).

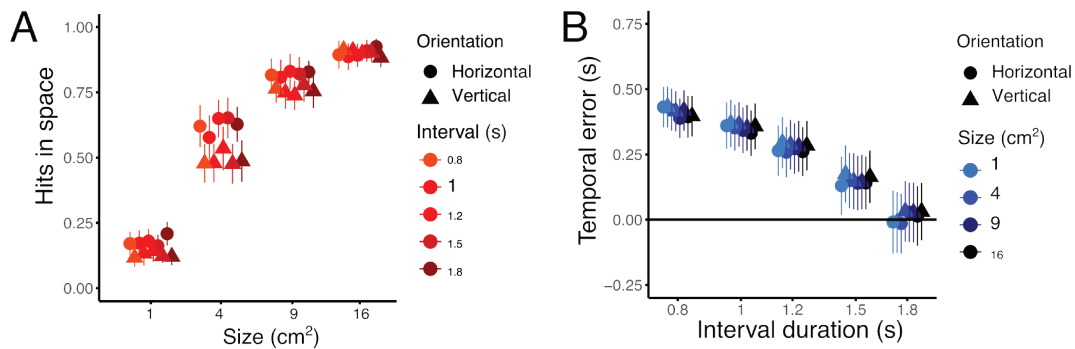


FIGURE 6.2: Spatial and temporal performance. (A). Proportion of spatial hits is plotted against stimulus size. Different interval durations are color coded (darker shades of red for longer durations) and the two target orientations are represented by different shapes (circles for horizontal and triangles for vertical). Performance increased linearly with the logarithm of target size. (B). Difference between hitting time (duration between the second target and the moment when participants ended their movement) and interval duration between the first two stimuli is plotted against the presented interval duration. Different colors represent different stimulus sizes (darker shades of blue for larger sizes) and different shapes represent the two target orientations. Temporal errors decreased linearly with the duration of the interval. Error bars represent standard error of the mean across participants.

#### 6.4.2 Synchronization to the temporal sequence is affected by interval duration and target orientation

We quantified performance on the synchronization task by calculating a temporal error between hitting time and presented duration. Hitting time was the temporal interval between the presentation of the second target and the moment when participant stopped moving. On Figure 6.2B, temporal errors are plotted against interval duration. We analyzed the results with a linear mixed effect model, with the logarithm of presented duration, target size, and orientation as within-subject

fixed effects. The dependent variable was the signed temporal error and, as random effects, we allowed intercepts and slopes of all predictors to vary for each subject to account for additional variability. The analysis showed that temporal error decreased significantly with the logarithm of presented duration (Wald Chi-square (1) = 45.01,  $p < 0.01$ ). Temporal error decreased when the logarithm of presented duration increased (slope = -1.136, SE = 0.170,  $t = -6.709$ ,  $p < 0.01$ ). Orientation had a small but significant effect on temporal error (Wald Chi-square (1) = 20.15,  $p < 0.01$ ), and temporal error was slightly larger for vertically oriented targets (slope = 0.15, SE = 0.005,  $t = 4.489$ ,  $p < 0.01$ ). There was no effect of target size (Wald Chi-square (1) = 0.264,  $p < 0.01$ ).

### 6.4.3 Confidence about the performance is affected by interval duration and target size

On each trial, we asked participants to estimate their confidence about their movement performance. More specifically, participants had to estimate if on a particular trial they were better or worse than on average of all previous trials. These binary responses are summarized in Figure 6.3 and plotted against interval duration. Since participants could see their hand, they had feedback about performance on a spatial component of the task. For that reason, for the analysis of confidence judgements, we used only trials in which the hand landed within the target (hits in space). We quantified the effects by means of a generalized linear mixed-effect model, with binary confidence judgement as the dependent variable. We included the logarithm of interval duration, target size, and orientation as predictors. Also, to account for the non-linearity of the effect of interval duration (see Figure 6.3), we included a quadratic term (duration<sup>2</sup>). The random structure consisted of random intercepts and slopes for the duration and size predictors on the subject level. Significant predictors of confidence judgements were logarithm of the target size (Wald Chi-square(1) = 7.90,  $p < 0.01$ ), and the squared duration (Wald Chi-square(1) = 47.833,  $p < 0.01$ ). Odds of being confident in performance on a given trial was increasing with the logarithm of target size (slope = 0.471,  $\exp(\text{slope}) = 1.60$ , SE = 0.160,  $z = 2.897$ ,  $p < 0.01$ ). In addition, we observed a non-linear relationship between interval duration and confidence (slope = -11.939, SE = 1.726,  $z = -6.916$ ,  $p < 0.01$ ).

### 6.4.4 How do participants perform the action?

We now analyse separately reaction time (a moment when participants started moving) and movement duration (duration from the movement onset to end of

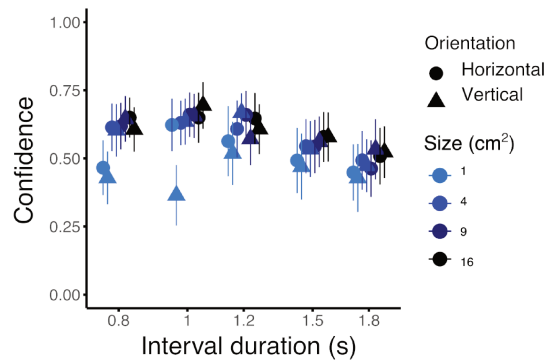


FIGURE 6.3: Proportion of trials estimated to have better than average performance is plotted against interval duration. Target sizes are represented by different colors and the two orientations by different shapes. Confidence about one's performance was larger for shorter durations and for larger targets. Error bars are standard error of the mean across participants.

the movement). Because the effects reported here are similar across target orientations, we pool the data across these two orientations. Reaction time and movement duration as a function of presented interval duration and target size are summarized in Figure 6.4A. Across increasing overall hitting times, we observe a general tendency to delay reaction time and relatively brief and constant movements.

To assess whether the way participants trade off reaction time and movement duration was affected by conditions in our experiment, we fitted a linear mixed-effect model with ratio between reaction time and movement duration as dependent variable, and logarithm of presented duration, size, and their interaction as continuous predictors, and orientation as factor. The ratio between reaction time and movement duration is a relative measure of how participants trade off reaction time and movement duration on a particular trial. Random structure consisted of both intercepts and slopes for interval duration and size to account for additional variability between participants. The results showed an effect of presented interval (Wald Chi-square(1) = 21.7,  $p < 0.01$ ), size (Wald Chi-square(1) = 13.52,  $p < 0.01$ ), and the interaction between the two predictors (Wald Chi-square(1) = 7.12,  $p < 0.01$ ). Orientation was not a significant predictor (Wald Chi-square(1) = 0.002,  $p = 0.96$ ). These results suggest that increasing both the duration of the interval (slope = 2.16, SE = 0.46,  $t = 4.659$ ,  $p < 0.01$ ) and the size (slope = 0.095, SE = 0.026,  $t = 3.677$ ,  $p < 0.01$ ) of the target leads to an increase in reaction time relative to movement duration. Moreover, since we observed a significant positive interaction between the predictors, the effects of the interval duration are different for different target sizes, namely the larger the size, the larger was the effect of interval duration on the trade-off (slope = 0.352, SE = 0.132,  $t = 2.66$ ,  $p < 0.05$ ). To further investigate how well people perceive, monitor and adjust movement duration while performing

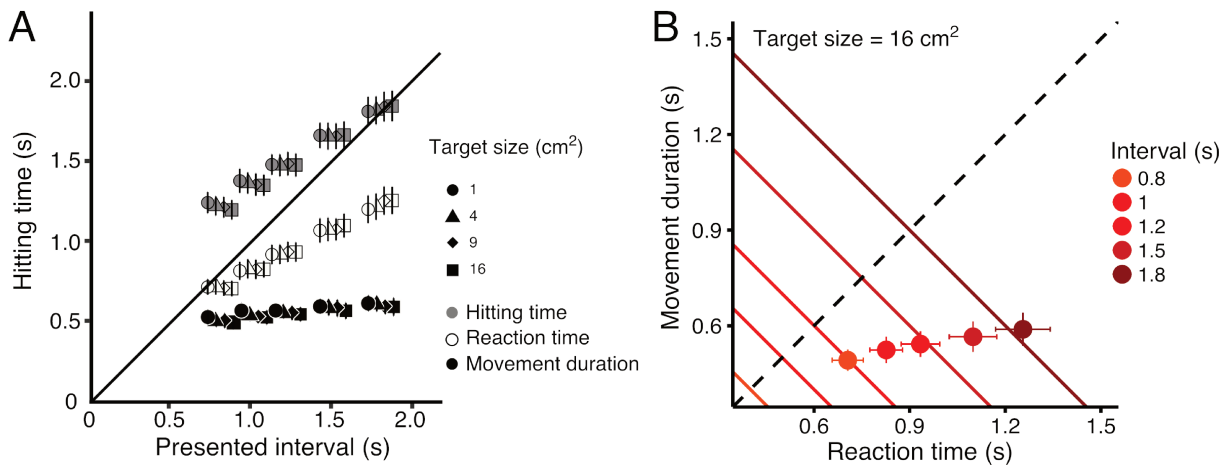


FIGURE 6.4: Contributions of reaction times and movement durations to hitting times. (A). Reaction time, movement duration and hitting time are plotted against interval durations for different target sizes. Results are averaged across participants and across the two target orientations. (B). Average movement duration are plotted against reaction time for the five different interval durations (darker shades of red indicate longer intervals). Only data for the largest target size are shown. Using the same color code, diagonal lines indicate the trade-off between reaction time and movement duration that are compatible with interval durations. On average, participants tended to delay the movement onset and make brief movements (data are below the identity dashed line where reaction times equaled movement durations). Most of the variability between conditions was due to different reaction times. Error bars indicate standard error of the mean across participants.

a movement. Since the target size affected movement duration in a predictable manner, we asked whether participants took this relationship into account when they planned the movement. If they did, we would expect differences in reaction time for different target sizes (small targets require longer movement durations, so reaction time should be shorter in these conditions). We observed an interaction between interval duration and target size on reaction time. Reaction time increased with both interval duration (Wald Chi-square(1) = 39.98,  $p < 0.01$ ) and target size (Wald Chi-square(1) = 3.948,  $p < 0.05$ ), and the increase was larger for larger durations and larger targets (Wald Chi-square(1) = 21.802,  $p < 0.01$ ).

To assess whether the way participants trade off reaction time and movement duration was affected by conditions in our experiment, we fitted a linear mixed-effect model with ratio between reaction time and movement duration as dependent variable, and logarithm of presented duration, size, and their interaction as continuous predictors, and orientation as factor. The ratio between reaction time and movement duration is a relative measure of how participants trade off reaction time and movement duration on a particular trial. Random structure consisted of both intercepts and slopes for interval duration and size to account for additional

variability between participants. The results showed an effect of presented interval (Wald Chi-square(1) = 21.7,  $p < 0.01$ ), size (Wald Chi-square(1) = 13.52,  $p < 0.01$ ), and the interaction between the two predictors (Wald Chi-square(1) = 7.12,  $p < 0.01$ ). Orientation was not a significant predictor (Wald Chi-square(1) = 0.002,  $p = 0.96$ ). These results suggest that increasing both the duration of the interval (slope = 2.16, SE = 0.46,  $t = 4.659$ ,  $p < 0.01$ ) and the size (slope = 0.095, SE = 0.026,  $t = 3.677$ ,  $p < 0.01$ ) of the target leads to an increase in reaction time relative to movement duration. Moreover, since we observed a significant positive interaction between the predictors, the effects of the interval duration are different for different target sizes, namely the larger the size, the larger was the effect of interval duration on the trade-off (slope = 0.352, SE = 0.132,  $t = 2.66$ ,  $p < 0.05$ ). To further investigate how well people perceive, monitor and adjust movement duration while performing a movement. Since the target size affected movement duration in a predictable manner, we asked whether participants took this relationship into account when they planned the movement. If they did, we would expect differences in reaction time for different target sizes (small targets require longer movement durations, so reaction time should be shorter in these conditions). We observed an interaction between interval duration and target size on reaction time. Reaction time increased with both interval duration (Wald Chi-square(1) = 39.98,  $p < 0.01$ ) and target size (Wald Chi-square(1) = 3.948,  $p < 0.05$ ), and the increase was larger for larger durations and larger targets (Wald Chi-square(1) = 21.802,  $p < 0.01$ ).

### 6.4.5 Model

In order to summarize the above results, we present a simple model that accounts for the main features of the participants' performance. First, we participants need to encode the presented interval duration between the first two stimuli. The uncertainty in the encoded interval is assumed to be normally distributed around the physical duration of the presented interval that is we assume that the estimated duration is unbiased. Following the scalar property of interval timing (Gibbon, 1977; Jazayeri & Shadlen, 2010), we assume that the variance of the estimated interval duration scales with interval duration. In other words, the variance is  $wf_I^2$  where  $I$  is the interval duration and  $wf$  is Weber fraction for perceived duration. The value of the  $wf$  was fixed to 0.1, based on the values found in the literature (Jazayeri & Shadlen, 2010).

Once the interval is encoded, the participant makes a decision when to start moving and for how long. We assumed that participants learned the ranges of possible interval durations and target sizes, and developed a strategy of how and

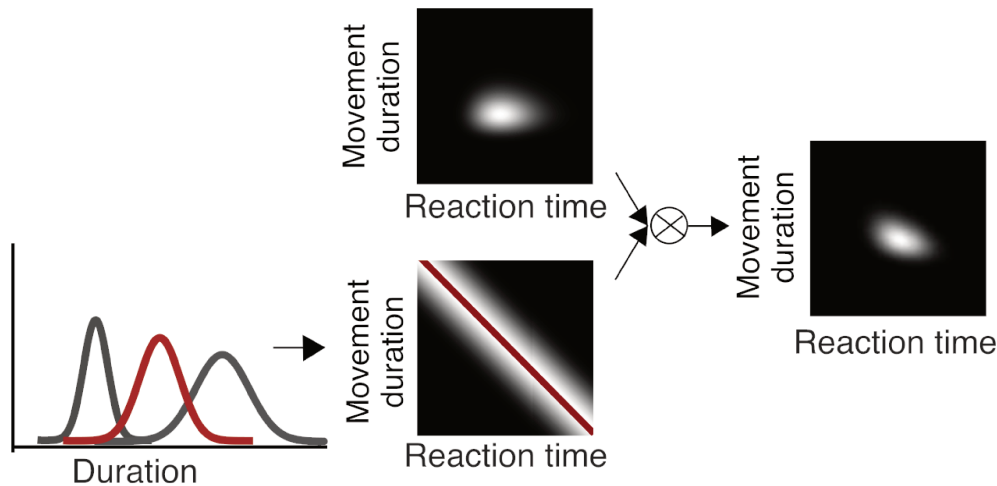


FIGURE 6.5: Schematic representation of the model. The joint a posteriori distribution of reaction time and movement duration (rightmost panel) is modeled as the combination of encoded duration (bottom middle panel) and a “motor prior” (upper middle). The encoded duration is modeled as a unimodal normal distribution centered on the presented duration and with variability that is growing with presented duration. The motor prior is a bivariate normal distribution in log reaction time and log movement duration space. The duration estimate is multiplied with the motor prior distribution to determine the final planned hitting time and the trade-off between reaction time and movement duration.

when to execute their hand movement. This expectation was modeled as a “motor prior”, a bivariate normal distribution on reaction time and movement duration. This motor prior reflects a propensity to produce stereotypical motor movements irrespective of the specific characteristics of each trial. Parameters of the distribution were free parameters in the model. The final planned movement onset and duration in each condition was obtained by multiplying the encoded duration and the motor prior distribution. To account for changes of movement duration with target size, we linearly scaled the movement duration mean of the prior distribution with respect to the target size. The scaling factor was obtained in a control experiment where we asked participants to reach to the targets with no temporal constraint. Since we found no effect of the target orientation on the trade-off, we did not include target orientation in the model.

As shown on Figure 6.6, the model successfully described performance of participants (median  $R^2$  for reaction time was 0.890, and movement duration 0.350). In other words, performance was well described with a single strategy across conditions, which we formalized as “motor prior” distribution. In comparison, a model without the prior can explain variability in reaction time ( $R^2 = 0.880$ ), but completely fails to capture variability in movement duration ( $R^2 = 0.110$ ).



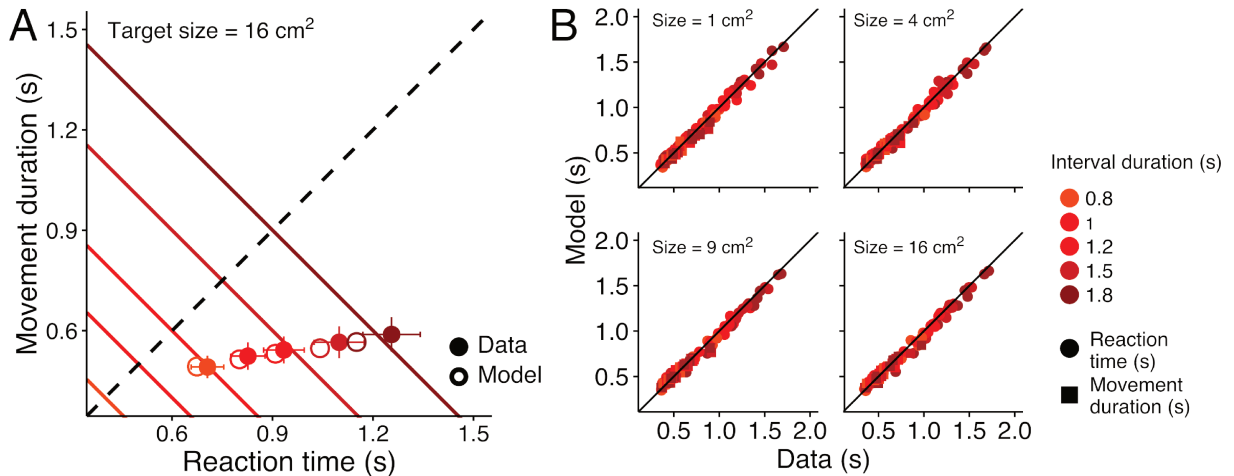


FIGURE 6.6: Comparisons of data and the model. (A). Average movement duration is plotted against reaction time, for the five interval durations (darker shades of red indicate longer interval durations). Only the largest size is shown in this plot. Data are shown with filled and model predictions with open symbols. The lines follow the same conventions as those shown in Figure 6.4. (B). Predicted mean reaction time and movement duration for each participant is plotted against the observed values. The four panels show data for the four target sizes. Reaction time is shown as circles and movement duration as square symbols.

#### 6.4.6 Does confidence in performance depend on the way we perform an action?

After executing each timed movement to a predictable target, participants estimated whether that movement was better or worse than the average movements they had executed so far. We are interested in the factors that contribute to this motor confidence judgment, focusing in particular on reaction time and movement duration. In the context of the model described above, we hypothesised that confidence was related to absolute deviations from a planned action. More specifically, participants could have assigned a low confidence to a trial that deviated strongly from the intended plan. The planned action, split between reaction time and movement duration, corresponds to the mean of the posterior distribution in our model. Alternatively, planned reaction times and movement duration can be simply estimated from the data by considering the mean reaction time and movement duration for each condition (Dean et al., 2007). Deviations from the means measure how badly the movement on a particular trial was different from the planned one. Therefore, for each participant, we calculated the absolute deviation from the mean of reaction time and movement duration for each condition. We tested our hypothesis by fitting the data with a general mixed-effect model. The dependent variable was the binary confidence judgement, and the absolute deviations in reaction time

and movement duration were predictors. We included a random structure that consisted of random intercepts and slopes for interval duration and target size on the level of participant. We observed an effect of the absolute deviation in reaction time (Wald Chi-square(1) = 19,  $p < 0.01$ ), but not for movement duration (Wald Chi-square(1) = 3.32,  $p = 0.07$ ) or their interaction (Wald Chi-square(1) = 0.32,  $p = 0.58$ ). The larger the absolute deviation from mean reaction time on a trial, the less confident participants were about the performance on that trial (slope = -1.12, SE = 0.31,  $z = -3.630$ ,  $p < 0.01$ ). To get a sense of the contribution of reaction time and movement duration on performance and confidence, we performed a quantiles analysis. For each participant, each interval duration and each target size condition, we split reaction times and movement duration in five equally sized bins. The relative frequency of pairs of reaction times and movement durations is shown in Figure 6.7A. The figure shows the trade-off between these two movement components (most data along the main diagonal), with some bias for the extremes corresponding to the combinations of large reaction time and small movement duration, and small reaction time and large movement duration. For each bin of reaction time and movement duration, we then computed the absolute temporal error for each condition and participant, and then averaged these errors (Figure 6.7B). Temporal error was largest for long reaction times and movement durations, which is consistent with the bias of arriving late to the target. We replicated the same analysis but replacing temporal errors by mean confidence judgments. The effects of deviation in reaction time and movement duration on confidence judgements, averaged across participants and conditions, are represented on Figure 6.7C. The effects on confidence are noisy, but low confidence seems to dominate in the left and right columns, consistent with the statistically significant effect of the absolute deviation in reaction time reported above.

## 6.5 Discussion

We investigated human performance in an intricate temporal motor task. Participants were asked to synchronize their arm movement with a predictable temporal sequence. Additionally, we imposed a spatial constraint by asking participants to end their movement inside a target of varying size. Finally, we asked participants to estimate how good their performance was on each trial, compared to their performance on all previous trials.

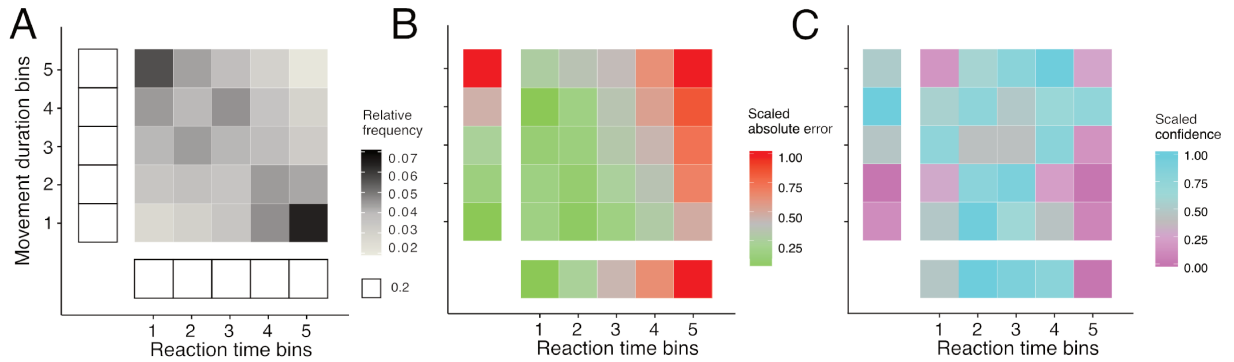


FIGURE 6.7: Temporal error and confidence judgements as a function of reaction time and movement duration. Distribution of reaction times and movement duration were binned in five equally sized bins, for each condition and each participant, and then averaged. Marginal distributions are shown above the x-axis (reaction time) and to the right of the y-axis (movement duration). (A). Relative frequency in each bin with a dominance over the main diagonal. (B). Distribution of temporal errors across different bins. Temporal error was largest for long reaction times and movement durations. (C). Average confidence about performance distribution. Only for the purpose of visualisation in this figure, absolute temporal error and confidence were scaled to the range between 0 and 1.

### 6.5.1 Reaction time and movement duration trade-off with different sources of uncertainty

Reaction time, movement duration and their trade-off, systematically varied with interval duration and target sizes, indicating that experimental manipulations were successful. Performance was better for longer durations, presumably because synchronizing with longer durations allowed for more time to plan and correct the movement. Furthermore, participants varied movement durations for aiming at targets of different sizes. Reaction time was longer for larger targets, to compensate for shorter movement duration. These results suggest that when planning a movement, both reaction time and movement duration are taken into account. However, participants mostly varied their reaction time, keeping movement duration brief and relatively constant across conditions. The bias increased with both interval duration and target size. The isochrony, or tendency to keep movement duration constant for different distances, is a well known principle in motor control (Engelbrecht, 2001; Freund, 1986; Viviani & Flash, 1995; Wolpert, 1997). Similar to the isochrony for spatial distance, our results are consistent with a tendency to keep movement durations constant across temporal intervals. Humans have an ability to use their knowledge of variability about their perception and movement in space (Trommershäuser et al., 2003) and time (Hudson et al., 2008) to properly plan and execute actions. However, the knowledge can be limited or biased (Maloney

& Zhang, 2010). The trade-off we observed suggests that participants either have incorrect representations of the variabilities of their reaction time and movement duration, or they are not minimizing the temporal variability when performing the task. Namely, participants systematically chose longer reaction times relative to movement duration in spite of the fact that variability scaled faster with reaction time than with movement duration (coefficients of variation for reaction time were larger than for movement duration,  $t(199) = 6.842$ ,  $p < 0.01$ ). The performance on the task was well described by a simple model involving a single motor strategy (“motor prior”) for different interval durations and target sizes. Why would participants adopt this strategy? Participants could aim at minimizing the perceived costs of their action, if not moving for longer time, rather than performing slow and long movements, is less costly (Cos et al., 2014, 2012; Dean et al., 2007). Alternatively, participants could perceive the movement onset as more controllable than the movement duration. Further work is needed to specifically address these hypotheses and disentangle the different sources of the observed bias.

### 6.5.2 Humans have biased estimates of confidence in their actions

Participants used different cues to estimate their confidence about their performance in a temporal synchronization task. Both the spatial and temporal errors were affected by the orientation of the target, and performance was better if target was oriented horizontally. However, confidence did not depend on the target orientation. Therefore, participants did not take into account all parameters that were affecting their performance. In an agreement with previous findings showing that humans do not always have an accurate representation of their spatial (Wu et al., 2006) or temporal (Mamassian, 2008) uncertainty, we observed that participants also failed to properly monitor the effect of the target shape on both spatial and temporal performance. The duration of the interval affected both performance on a temporal aspect of the task and confidence, but in opposite directions. Performance was better for longer durations, but participants were less likely to be confident on those trials. Since shorter intervals are encoded with less uncertainty (Gibbon, 1977; Jazayeri & Shadlen, 2010), we could assume that participants were using sensory uncertainty as one of the cues for estimating confidence in their actions. These findings are in an agreement with the evidence that metacognitive judgements rely on complex mechanisms that integrate multiple sources of information (Barthelmé & Mamassian, 2010; de Gardelle & Mamassian, 2014).

### **6.5.3 Accuracy and confidence can be dissociated for timing an action**

Confidence judgements were affected by absolute deviations in reaction time, but not movement duration. The finding is in disagreement with previous studies showing good error monitoring for temporal judgements (Akdoğan & Balci, 2017). One of the differences between this previous work and the one presented here, is that in the former, movement duration and its contribution to reproduced duration was minimal. In contrast, in our task, as in daily life, participants had to integrate information about both reaction time and movement duration to properly time their action. The latter is a more demanding, which could explain why participants were less successful. Our results are relatively well explained by a simple model, where deviations from the planned (posterior) distribution for reaction time, but not movement duration, are used as confidence evidence. The analysis of reaction times and movement durations showed that when planning an action, movement duration is taken into account, and reaction time is adjusted accordingly. However, once the movement is executed, different components of the movement do not contribute equally to the metacognitive judgement. Therefore, humans are either bad at estimating differences between actual and planned duration of the movement, or do not take this information into account when estimating confidence. Limited access to the movement execution is consistent with the sensory attenuation hypothesis. More specifically, if sensory information is suppressed during the movement execution (Blakemore et al., 2000; Cardoso-Leite et al., 2010; Wolpert, 1997), it would reduce the available information about the movement that would inform confidence estimation. Furthermore, these results are in an agreement with the evidence that information about movement onset and offset could originate from different brain structures (MacKinnon & Rothwell, 2000). If the metacognitive judgement has access to cortical information only (Kepecs et al., 2008; Kiani & Shadlen, 2009), it would have limited or indirect access to information about different stages of movement planning and execution. It is important to note that we asked participants to evaluate their performance on both spatial and temporal aspect of the task. We chose this design to encourage participants to be spatially accurate, and adjust their movement durations for different target sizes. Because participants could see their hand, they received an immediate feedback about their spatial performance. If visual feedback was not provided, it is possible that participants could have used a mixture of strategies to estimate their performance. Further work is needed to address this issue in a greater detail.

## 6.6 Supplementary analyses

One reasonable concern is that when self-estimating the performance, participants evaluated the sensory uncertainty (the longer the interval, the greater the uncertainty), rather than the sensorimotor performance. Indeed, the relationship between the average confidence and the interval duration (Figure 6.3) suggests that they could have used this information to evaluate their performance. Nevertheless, although we cannot exclude this possibility, self-estimation of the performance was not entirely based on the sensory uncertainty. As shown in the Figure 6.3, the confidence scaled positively with the target size, that was not related to the temporal sensory uncertainty. To show further evidence for the hypothesis that participants considered movement execution, rather than only sensory uncertainty, tested whether the confidence depended on the absolute temporal error as well as spatial performance. In Figure 6.8 average confidence is plotted against binned absolute temporal error, separately for the two spatial performance outcomes. Performance self-evaluation depended on the spatial outcome of the movement, indicating that participants also included this aspect of the performance when self-evaluating the performance.

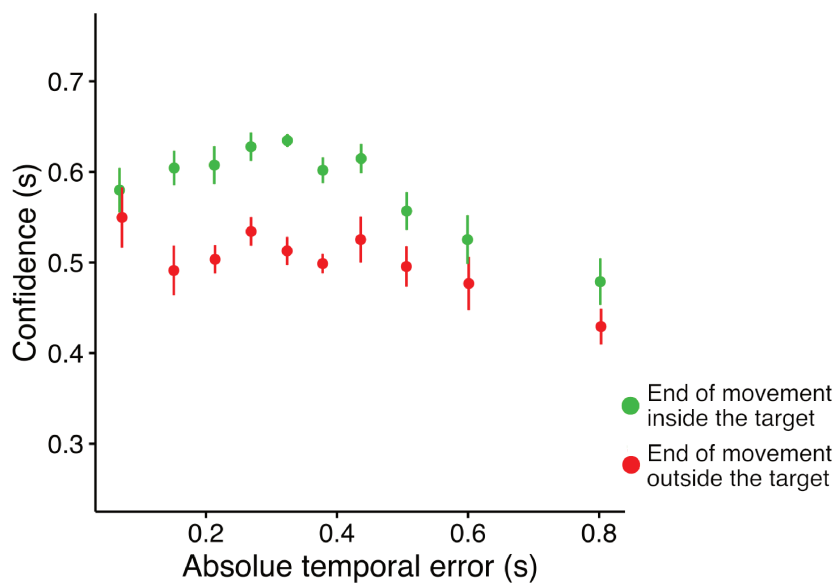


FIGURE 6.8: Average performance self-estimation, as a function of absolute temporal error, split for the trials for which the movement was spatially correct (movement ended inside the target, shown in green), and incorrect (green). The performance was self-estimated as worse than average on trials with greater absolute temporal error, and trials in which movement in which the target was missed.

### 6.6.1 Timing an action affects online movement correction

We observed that confidence judgements were not equally sensitive to all aspects of the movement execution. These findings raise a question of how well people perceive, monitor and adjust movement duration while performing a movement. In order to answer this question, we examined two different aspects of our data. First, since the target size affected movement duration in a predictable manner, we asked whether participants took this relationship into account when they planned the movement. If they did, we would expect differences in reaction time for different target sizes (small targets require longer movement durations, so reaction time should be shorter in these conditions). We observed interaction between interval duration and size of the target on reaction time. Reaction time was increasing with both interval duration (Wald Chi-square(1) = 39.98,  $p < 0.01$ ) and target size (Wald Chi-square(1) = 3.948,  $p < 0.05$ ), but the increase was larger for larger durations and targets (Wald Chi-square(1) = 21.802,  $p < 0.01$ ). This result suggests that people do take into account differences in movement duration when planning an action. Second, we assessed whether participants made online corrections of their movements by analyzing the position variability at different stages of the movement (Cameron & López-Moliner, 2015; Khan & Franks, 2003). The aim of this analysis was to assess whether participants were monitoring and correcting their movement online, or they executed movements programmed in advance. In this analysis, an increase of variability in position with movement duration is assumed to correspond to accumulation of noise and feedforward processing. Reduction of variability towards the end of the movement suggests corrections mediated by online feedback (Khan & Franks, 2003). We normalized movement duration on each trial, by dividing it in ten bins of equal duration. For each bin we calculated variability across trials separately for each condition of our experiment. This allowed us to compare movements with different movement durations and speeds in a continuous manner, without relying on localization of kinematic markers, which can be difficult to obtain (Cameron & López-Moliner, 2015). Finally, since our main interest was in investigating how people time their actions, we compared variability profiles in the main experiment with those in a control experiment where participants were asked to point to a target without any temporal restrictions. Since in the control experiment we used only two extreme target sizes and the two orientation, we compared performance only for those conditions, and averaged across different durations of the main experiment. On Figure 6.6 variability on x and y axis of the movement is plotted as a function of binned movement duration and target size, for the two experiments.

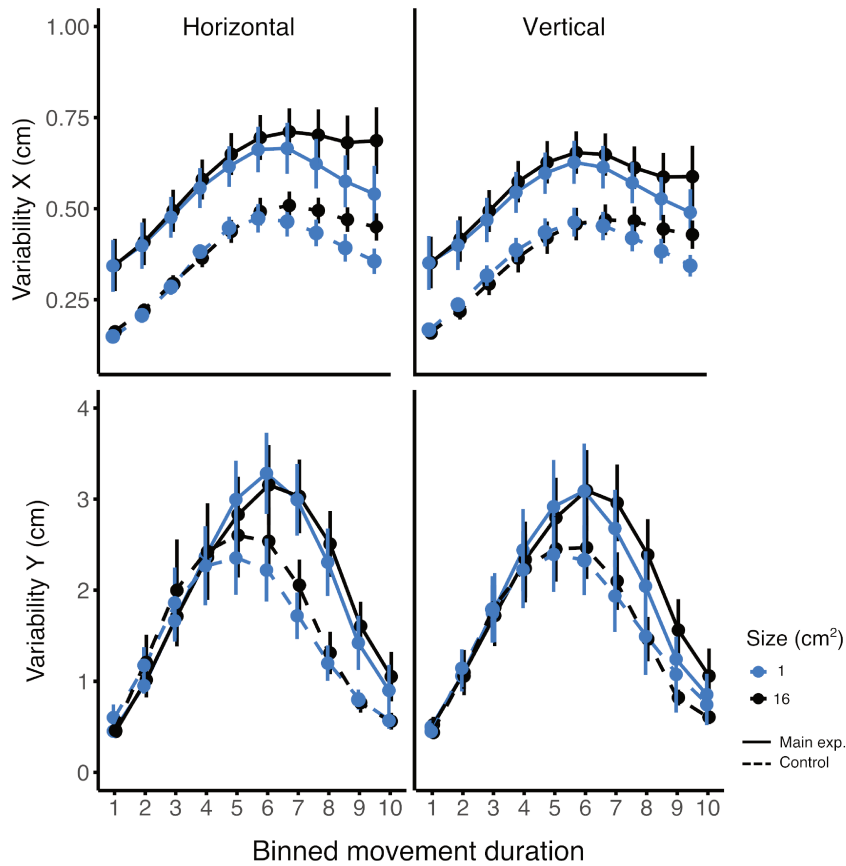


FIGURE 6.9: Spatial variability profiles for x (top row) and y-axis (bottom row) of the movement, plotted separately for the main experiment and the control experiment (full and dashed lines, respectively). Color codes for the two target sizes and plots for the two target orientations are shown on different panels. Error bars correspond to standard error of the mean across participants.

We tested whether variability profiles between the main and the control experiment were different by means of two repeated measures ANOVA with experiment, binned movement duration, size and orientation as factors, and variability in x and y direction as dependent variables. Variability on the x-axis was significantly smaller for control experiment ( $F(1,8)=11.13$ ,  $p<0.01$ ), and different for different movement duration bins ( $F(1,8)=29.62$ ,  $p<0.01$ ). We observed an effect of target size ( $F(1,8)=12.5$ ,  $p<0.01$ ) and orientation ( $F(1,8)=7.067$ ,  $p<0.05$ ). Also, there was an interaction between movement duration bin and target size ( $F(1,8)=31.41$ ,  $p<0.01$ ) and orientation ( $F(1,8)=32.72$ ,  $p<0.01$ ). However, there was no interaction between experiment and temporal marker. In other words, the rate of change in the variability with time was the same for the two experiments. For variability profiles on the y-axis we observed main effect of the experiment ( $F(1,8)=12.35$ ,  $p<0.01$ ) and significant interaction between experiment and movement duration bin ( $F(1,8)=13$ ,  $p<0.01$ ). Interaction between temporal marker and the experiment means that the



rate of change in variability with movement duration was different in the two experiments. Also there was a small but significant three-way interaction between experiment, movement duration bin and orientation ( $F(1,8)=9.53$ ,  $p<0.05$ ). As the second measure of online control we calculated proportion of movement duration after the peak velocity. This analysis relies on an assumption that the longer the time after peak velocity on a particular trial, the greater the online control of the movement (Cameron & López-Moliner, 2015; Elliott, Helsen, & Chua, 2001). The proportion of the movement duration after the peak velocity was considerably larger in the main experiment compared to the control ( $F(1,8) = 78.78$ ,  $p<0.01$ ) and for smaller targets compared to the larger ones ( $F(1,8) = 16.39$ ,  $p<0.01$ ).

To investigate whether variability in the movement execution was related to confidence judgements, we contrasted variability profiles for trials estimated as “performance better than average” and “performance worse than average”. On Figure 6.7 variability on y (primary direction of the movement) and x axis are plotted as a function of binned movement duration and confidence judgement.

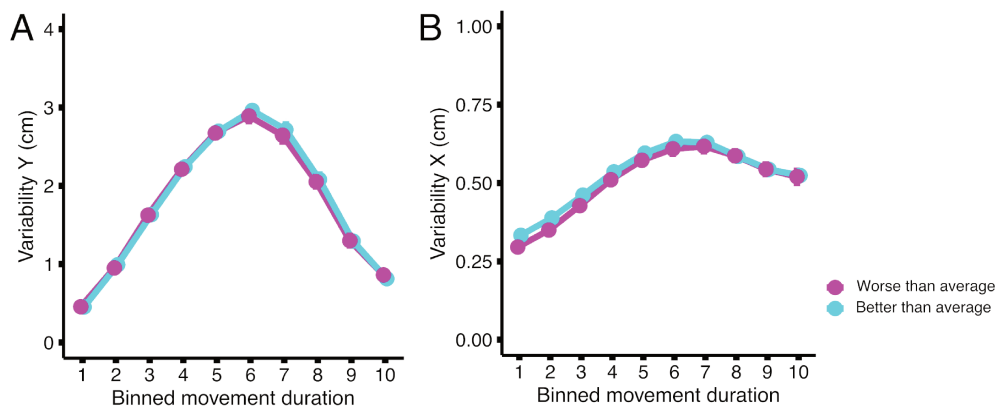


FIGURE 6.10: Variability profiles on x (panel A) and y (panel B) axis, plotted separately for trials reported as “performance better ” and “performance worse than average”. Data are averaged across interval durations, size and orientation. Error bars represent standard error of the mean across participants

To quantify the effect, we analysed the data with two linear mixed-effect models, with binned movement duration and confidence as factors, and variability in x and y direction as dependent variables. Random structure included subject intercepts and slopes for interval duration, size and orientation. In the primary axis of the movement (y-axis) we observed no interaction between confidence estimation and movement bin, meaning participants were not performing movement differently in the two conditions (Wald Chi-square(1) = 0.0795,  $p = 0.7780$ ). In the x-axis, we observed an interaction between confidence estimation and movement duration bin (Wald Chi-square(1) = 9.2832,  $p < 0.01$ ). However, as shown on Figure 6.8,

the different effect of confidence response relative to different movement duration bins was at the beginning of the movement.

## 6.7 Conclusion

In this chapter I presented an experiment that explored how participants time and perform an action and how the action is self-evaluated. The findings indicate that when performing the movement, participants had a strategy to delay the movement, and perform short movements. The bias was more pronounced for larger targets and longer intervals, indicating that it was not simply the consequence of inability to move quick enough (for very short intervals). Participants were also asked to self-evaluate their performance. These estimates were sensitive to actual performance, and were related to interval duration and target size. The findings suggest that participants were not good at estimating how their movement duration affected the performance. There was, however, considerable variability between participants, and these results are not as consistent as those for the performance. Although meta-cognitive judgements are known to be more variable (de Gardelle & Mamassian, 2014), it is possible that our choice of the task, or complexity of the experimental situation (different size, durations and orientations interleaved), contributed to the variability. Therefore, it is crucial to pursue this question in a greater detail, with insights provided by the study presented here. On the other hand, in real life we are exposed to a noisy, cluttered and to a certain extent unpredictable environment. That said, it seems that self-evaluation of the temporal performance can be more difficult than suggested by previous studies (Akdoğan & Balci, 2017). This study provided us with guidelines for the future work, and pinpointed some issues to be further addressed. In particular, if we want to investigate how humans perceived duration or anticipate events in time, simple reproduction tasks, with response time may be sufficient. If we want, however, to understand how humans behave in the environment, we need to design the tasks in a manner that will provide us with insights into how the perceived time is transformed into movement (Brenner & Smeets, 2015).





## Chapter 7

# Conclusions

The experimental work presented in my thesis investigated different aspects of human time behavior. In this final chapter, I will summarize the main findings from the three avenues of research presented in the thesis. Furthermore, I will go beyond the reported results, to discuss perspectives for future work motivated by the main findings.

## 7.1 Main findings

The work presented in the **Part 1** was motivated by an assumption of the prominent models of time (duration) estimation: the resetting of the timing mechanism. More specifically, I investigated duration perception of a visual event without an explicit clock reset. A novel stimulus was designed to address this question. The accuracy and precision of perceived durations were tested in two conditions: durations with clear, salient onsets, and durations with implicit onsets, that were revealed retrospectively. The two hallmarks of time perception were found in both conditions: the scalar variability of time and the regression to the mean. However, effects were different for the two conditions: the temporal context affected the estimates more in the *implicit* onset condition, and the estimates were more biased towards the mean of the presented durations. Temporal discrimination sensitivity was larger in the *explicit* relative to the *implicit* onset conditions, in agreement with accounts of the effect of temporal context on this bias (Jazayeri & Shadlen, 2010).

This study has an important implication. In life outside the laboratory, we often do not know when relevant events will start, and probably our behavior is more similar to the task in which the onset of the duration is revealed retrospectively. Since the findings show that in these conditions the temporal estimation is more variable and biased, studies investigating prospective timing could be overestimating the performance in temporal tasks.

The temporal estimates in both conditions were biased towards the mean of the presented range of durations, and their variability scaled with the presented duration. On one hand, these effects are the principles found in sensory (and magnitude) estimation in general. A great body of research showed that prospective time perception complies to the Weber's law and regression to the mean (Lejeune & Wearden, 2009b; Rammsayer, 1994; Rammsayer & Vogel, 1992). Here I also reported that this is true for temporal estimates that are that are made retrospectively, at least to some extent. On the other hand, given that these are general principles found across different domains of perception, the fact that they were found in both conditions does not necessarily imply shared mechanism or representation. A possible future direction is to investigate what cues are used for estimating interval durations in the two tasks. For example, it is known that the speed of stimuli in motion affects temporal estimates (Kanai, Paffen, Hogendoorn, & Verstraten, n.d.; Kaneko & Murakami, 2009; Linares et al., 2016). In addition, a recent study showed that when estimating time to contact of a moving object, humans integrate speed

and temporal information to optimize performance (Chang & Jazayeri, 2018). Investigating the cues relevant for the performance in the two tasks would provide evidence for whether they share common mechanisms.

A recent study showed that in a free foraging task, the lateral entorhinal cortex of mice encoded the temporal information inherently, across different time scales (Tsao et al., 2018). Interestingly, even this spontaneously encoded temporal information scaled with the uncertainty of the context. Therefore, it would also be interesting to investigate how the uncertainty of the temporal context affects judgments in the *implicit* onset task.

In **Part 2** of the thesis, I presented three studies that investigated the effects of the context on the perceived time of visual and auditory events. The studies presented in **Chapters 4** and **Chapter 5** were motivated by the previous work demonstrating that the perceived time of an event is affected by stimuli from the same (Burr et al., 2013; Karmarkar & Buonomano, 2007a; Nakajima, Ten Hoopen, et al., 1992) and different modalities (Burr et al., 2009; Hartcher-O'Brien & Alais, 2011; Roach et al., 2006; Vidal, 2017). I investigated whether the biases induced by the temporal context are mandatory.

The experiments presented in **Chapter 4** tested whether the moment when a visual event is perceived depends on other visual stimuli presented before or after it. The target was revealed either after the trial had ended, or it was cued beforehand, by its color or temporal order. Interestingly, the perceived time of the target depended on the cueing method. The perceived time of the target was attracted to the presented time of the distractor when the target was revealed at the end of the trial, and both events were equally attended. When the target was cued beforehand, the reported time was under or overestimated, depending on whether the properties of the distractor had to be decoded (pre-cued by color) or not (pre-cued by order). To the best of my knowledge, these effects are not accounted for by dedicated temporal mechanisms. The State Dependent Network model, on the other hand, predicts that (at least for brief durations) stimuli preceding the target would change the state of the network, and bias temporal estimates. The finding that the distractors presented both before and after the target have an effect on the perceived time of stimuli are not consistent with this hypothesis. Nevertheless, it is possible that a different mechanism is responsible for the biases induced by the distractors preceding and following the target. It seems that this is indeed the case for the effects of the distractor on the perceived position in space (Chien et al., 2011; Chow et al., 2014; Ono & Watanabe, 2011; Suzuki & Cavanagh, 1997).



In **Chapter 5** I tested multisensory temporal interactions between asynchronous auditory and visual stimuli. The results showed that even when attending to a stimulus from one modality, participants could not ignore the conflicting temporal information from the other modality. These results are in agreement with previous work, that indicates mandatory interactions for the perception of rhythm (Vidal, 2017) and rate (Roach et al., 2006). There was, however, considerable variability between participants. Although it is possible that these inconsistencies arise from the task used, the previous work showed that different participants do adopt different strategies for the combination of cues (Adams, 2016; Locke & Landy, 2017; Wozny et al., 2010).

The findings from these two projects suggest that the perceived time of events can easily be biased by other events presented before or after them. However, are the interactions of stimuli from different modalities based on the same mechanisms as the interactions between two stimuli from the same modality? Although it has been shown that cues between and within modalities are combined differently (Hillis, Ernst, Banks, & Landy, 2002b), there is some evidence that temporal interactions and integration can be similar within attributes and across modalities. It has been shown that the binding thresholds for cross-attribute (e.g. orientation and color) and cross-modal pairs are similar: around 2 -3 Hz (Fujisaki & Nishida, 2010). These findings suggest that both cross-attribute and cross-modal binding are mediated by a slow central process. In addition, in a visual search task, the effects of distractors on the detection of audio-visual synchrony can be eliminated by spatial cueing (Fujisaki, Koene, Arnold, Johnston, & Nishida, 2006).

The perceived time of events across the visual field is investigated in **Chapter 6**. The study was inspired by a fundamental question: what information is used by the brain to estimate when an event is perceived? Participants showed a bias to report events in the periphery earlier. Findings in this study support the hypothesis that the perceived time of (visual) events does not always correspond to the perceptual latencies measured in reaction time tasks. In addition, it suggests that the saliency of events may be relevant for estimating when something happened. In conjunction with the findings concerning the effect of salient spatial features on perceived time, presented in the Appendix of Part 2, these results support the hypothesis that saliency is an important cue for perceived time. Nevertheless, the bias reported here, along with other findings of different perceived time (duration) across the visual field, are not well understood.

The experimental evidence concerning metacognition in the context of time perception is scarce. Metacognitive judgements can, however, provide important insights into how certain computations are implemented in the brain (Mamassian, 2016). In **Part 3** I investigated anticipated time in the context of movement preparation and execution. In addition, participants reported their confidence in their performance. Results showed that when timing a movement of different durations, participants mostly varied their reaction time, keeping the average movement duration short and relatively constant across the conditions. Confidence judgments had a complex relationship with parameters in the task, and were predicted by absolute deviations in reaction time, but not movement duration. These results should be supported by further evidence. In particular, it would be important to design the task in manner that movement duration is varied to a greater extent in order to further test the hypothesis that movement duration is self-estimated differently from reaction time. Furthermore, the relation between reaction time and movement duration found in this experiment should be explained. A possible explanation for the observed bias in movement execution is that timing movement duration is more costly, in terms of different biomechanical costs. Although it is difficult to explicitly manipulate them experimentally, future work should investigate variables that affect the movement execution in timing tasks, by varying task requirements (e.g. by restricting movement trajectories, or by adding obstacles).

The close relationship between the perceived time and attention has been acknowledged for a long time (Nobre & Coull, 2010). Attention affects sensory processing in different ways (Carrasco, 2011). While spatial cueing enhances performance in various tasks, attending to a stimulus often produces biases of the perceived time. For example, attention grabbing or attended stimuli are perceived earlier or lasting for a long time (Eagleman, 2008; Spence & Parise, 2010; Tse et al., 2004). Our results are in agreement with these findings: attending to color or temporal order of stimuli, as well as presence of salient features bias reported time of visual events.

Moreover, human ability to detect, discriminate or reproduce immediate sensory experience is inevitably related to memory. However, as far as the time perception is concerned, this relationship may be particularly close. It is pertinent to understand how the temporal processing is related to other cognitive functions: what computations are carried out by the temporal processing mechanism, and how and at what stage of processing it interacts with other functions. There have been some efforts to integrate temporal processing in the broader theories of cognition (Staddon, 2005; Taatgen, Van Rijn, & Anderson, 2007). The multitude of

temporal behaviors and functions make this endeavour very demanding. Nevertheless, it could be crucial for understanding computations and making hypothesis about neural implementations of the timing mechanisms.

## 7.2 Is there time constancy?

Temporal context recalibrates behavior in time tasks, as well as the neural encoding of temporal information (Jazayeri & Shadlen, 2010; Miyazaki et al., 2005; Tsao et al., 2018). The findings reported in this thesis contribute to the great body of literature demonstrating how malleable human time perception is. Perceived duration is affected by the range of durations presented, and is even more biased when the onset of the duration is determined retrospectively. On the other hand, even when we know in advance which stimulus in a sequence of two we will be asked to report, our estimates are biased. In addition, a single event, from the same or different modality, presented before or after the attended stimulus, can bias perceived time. So what happens in life outside the laboratory? If we would extrapolate these findings, one could think that human time perception is so vulnerable to corruption from contextual information that it is rendered useless for explicit estimation and action planning. Nevertheless, we do manage to organize our experience in time, for immediate actions, or in memory. I will present two pieces of evidence that support this claim: precision of the motor system and constancy of the perceived duration.

There is a remarkable precision of our motor system in interception tasks (Brenner & Smeets, 2015). Dissociation between perception and action is an interesting but controversial topic (N. Bruno, 2001; Franz, 2001; Franz, Gegenfurtner, Bühlhoff, & Fahle, 2000; Goodale & Humphrey, 1998; Smeets, Brenner, de Grave, & Cuijpers, 2002). Although disputed for some phenomena, there is a great body of evidence showing that temporal precision for interception is greater than that of explicit temporal judgements (Brenner & Smeets, 2010, 2015). In particular, during interception, humans integrate various sources of information, including, but not limited to, the temporal information (Brenner & Smeets, 2015; Chang & Jazayeri, 2018). This difference suggests that humans effortlessly extract and integrate different cues to optimize their performance in timing tasks. When various cues are missing, and action is planned based on the temporal information only, both precision and variability of the action is compromised.

Given that time is so malleable, is there time constancy? In particular, can the perceived time be invariant to changes in external variables? To my knowledge,

only one study (Lisi & Gorea, 2016) has demonstrated a constancy for time perception. In this study, participants estimated the duration of a moving stimulus, with or without perspective cues. The constancy of perceived duration was found only for stimuli in the former case, when the visual stimulus was presented with a simplistic environmental cues. When designing an experiment researchers usually aim to reduce or eliminate all the features of the task and stimulus that are not of the immediate interest for the study. One could argue that this strategy leads to impoverished stimuli and context, too simplistic to capture the robustness of time perception. In other words, different cues that are used to robustly estimate temporal properties are removed, and time constancy fails. Future work should address this issue, by comparing the conditions in which the time perception is robust to changes in the context, and when it fails, and what cues are used to maintain it will provide important insights into the computations underlying it (Landy & Johnston, 1995).

In summary, in this thesis I explored different aspects of the human temporal behavior. The findings reported in the thesis revealed mandatory interactions between the perceived time of events and other events presented in their temporal proximity. In addition, they confirm the close relationship between the perceived time of events and the manner in which we attend to the events of interest. Finally, the findings indicate that certain processes, such as time needed to estimate the color of the stimulus or to execute movement, are not well accounted for when estimating time. In the different projects, great attention was devoted to designing novel and modifying tasks previously used in the literature, which enabled me to address important questions, such as the role of the prospective salient onset of events that are timed, or when events are perceived to have happened. Future work will address more directly how these computations are implemented to form a consistent and robust representations of events in time.



## References

- Acerbi, L., Wolpert, D. M., & Vijayakumar, S. (2012). Internal Representations of Temporal Statistics and Feedback Calibrate Motor-Sensory Interval Timing. *PLoS Computational Biology*, *8*(11). doi: 10.1371/journal.pcbi.1002771
- Adams, W. J. (2016). The Development of Audio-Visual Integration for Temporal Judgements. *PLoS Computational Biology*, *12*(4), 1–17. doi: 10.1371/journal.pcbi.1004865
- Addyman, C., French, R. M., & Thomas, E. (2016). Computational models of interval timing. *Current Opinion in Behavioral Sciences*, *8*, 140–146. doi: 10.1016/j.cobeha.2016.01.004
- Aedo-Jury, F., & Pins, D. (2010). Time compression increases with eccentricity: a magnocellular property. *Neuroreport*, *21*(2), 84–89.
- Agostino, P. V., Do Nascimento, M., Bussi, I. L., Eguía, M. C., & Golombek, D. A. (2011). Circadian modulation of interval timing in mice. *Brain Research*, *1370*, 154–163. doi: 10.1016/j.brainres.2010.11.029
- Ahissar, M., & Hochstein, S. (1997). Task Difficulty and the Specificity of Perceptual Learning. *Letters to Nature*, *387*, 401–406.
- Akdoğan, B., & Balci, F. (2017). Are you early or late?: Temporal error monitoring. *Journal of Experimental Psychology: General*, *146*(3), 347–361. doi: 10.1037/xge0000265
- Alais, D., & Burr, D. (2004). Ventriloquist Effect Results from Near-Optimal Bimodal Integration. *Current Biology*, *14*(3), 257–262. doi: 10.1016/S0960-9822(04)00043-0
- Alais, D., & Carlile, S. (2005). Synchronizing to real events: Subjective audiovisual alignment scales with perceived auditory depth and speed of sound. *Proceedings of the National Academy of Sciences*, *102*(6), 2244–2247. doi: 10.1073/pnas.0407034102
- Albright, T. D., & Stoner, G. R. (2002). Contextual Influences on Visual Processing. *Annual Review of Neuroscience*, *25*(1), 339–379. doi: 10.1146/annurev.neuro.25.112701.142900
- Alexander, I., Thilo, K. V., Cowey, A., & Walsh, V. (2005). Chronostasis without voluntary action. *Experimental Brain Research*, *161*(1), 125–132. doi: 10.1007/s00221-004-2054-3

- Allan, L. G. (1979). The perception of time. *Perception & Psychophysics*, 26(5), 340–354. doi: 10.3758/BF03204158
- Allan, L. G., & Gibbon, J. (1991). Human bisection at the geometric mean. *Learning and Motivation*, 22(1-2), 39–58. doi: 10.1016/0023-9690(91)90016-2
- Allman, M., Teki, S., Griffiths, T. D., & Meck, W. H. (2014). Properties of the Internal Clock: First- and Second-Order Principles of Subjective Time. *Ssrn*(January). doi: 10.1146/annurev-psych-010213-115117
- Amano, K., Johnston, A., & Nishida, S. (2007). Two mechanisms underlying the effect of angle of motion direction change on colour-motion asynchrony. *Vision Research*, 47(5), 687–705. doi: 10.1016/j.visres.2006.11.018
- Amano, K., Nishida, S., & Takeda, T. (2004). Enhanced neural responses correlated with perceptual binding of color and motion. *Neurology & Clinical Neurophysiology: NCN*, 2004, 48.
- Arao, H., Suetomi, D., & Nakajima, Y. (2000). Does time-shrinking take place in visual temporal patterns? *Perception*, 29(7), 819–830. doi: 10.1068/p2853
- Arnold, D. H. (2010). Relative timing and perceptual asynchrony. In R. Nijhawan & B. Khurana (Eds.), *Space and time in perception and action*. Cambridge University Press, Cambridge, U.K.
- Arnold, D. H., & Clifford, C. W. G. (2002a). Determinants of asynchronous processing in vision. *Proceedings of the Royal Society B: Biological Sciences*, 269(1491), 579–583. doi: 10.1098/rspb.2001.1913
- Arnold, D. H., & Clifford, C. W. G. (2002b). Determinants of asynchronous processing in vision. *Proceedings of the Royal Society B: Biological Sciences*, 269(1491), 579–583. doi: 10.1098/rspb.2001.1913
- Arnold, D. H., & Wilcock, P. (2007). Cortical processing and perceived timing. *Proceedings of the Royal Society B: Biological Sciences*, 274(1623), 2331–2336. doi: 10.1098/rspb.2007.0576
- Arrighi, R., Alais, D., & Burr, D. (2005). Perceived timing of first- and second-order changes in vision and hearing. *Experimental Brain Research*, 166(3-4), 445–454. doi: 10.1007/s00221-005-2384-9
- Aschoff, J. (1998). Human perception of short and long time intervals: Its correlation with body temperature and the duration of wake time. *Journal of Biological Rhythms*, 13(5), 437–442. doi: 10.1177/074873098129000264
- Ayhan, I., Bruno, A., Nishida, S., & Johnston, A. (2009). The spatial tuning of adaptation-based time compression. *Journal of Vision*, 9(11), 2–2.
- Ayhan, I., Bruno, A., Nishida, S., & Johnston, A. (2011). Effect of the luminance signal on adaptation-based time compression. *Journal of Vision*, 11(7), 22. doi: 10.1167/11.7.22

- Ayhan, I., Revina, Y., Bruno, A., & Johnston, A. (2012). Duration judgments over multiple elements. *Frontiers in Psychology, 3*(NOV), 1–8. doi: 10.3389/fpsyg.2012.00459
- Azzopardi, P., Jones, K. E., & Cowey, A. (1999). Uneven mapping of magnocellular and parvocellular projections from the lateral geniculate nucleus to the striate cortex in the macaque monkey. *Vision Research, 39*(13), 2179–2189. doi: 10.1016/S0042-6989(98)00319-8
- Bachmann, T., Pöder, E., & Luiga, I. (2004a). Illusory reversal of temporal order: The bias to report a dimmer stimulus as the first. *Vision Research, 44*(3), 241–246. doi: 10.1016/j.visres.2003.10.012
- Bachmann, T., Pöder, E., & Luiga, I. (2004b). Illusory reversal of temporal order: The bias to report a dimmer stimulus as the first. *Vision Research, 44*(3), 241–246. doi: 10.1016/j.visres.2003.10.012
- Bangert, A. S., Reuter-Lorenz, P. A., & Seidler, R. D. (2011). Dissecting the clock: Understanding the mechanisms of timing across tasks and temporal intervals. *Acta Psychologica, 136*(1), 20–34.
- Barthelmé, S., & Mamassian, P. (2010). Flexible mechanisms underlie the evaluation of visual confidence. *Proceedings of the National Academy of Sciences, 107*(48), 20834–20839.
- Bates, D., Maechler, M., Bolker, B., Walker, S., Haubo, R., Christensen, B., . . . Green, P. (2018). Package 'lme4'.
- Bates, D., Maechler, M., Bolker, B., Walker, S., et al. (2014). lme4: Linear mixed-effects models using eigen and s4. *R package version, 1*(7), 1–23.
- Battaglia, P. W., & Schrater, P. R. (2007). Humans trade off viewing time and movement duration to improve visuomotor accuracy in a fast reaching task. *Journal of Neuroscience, 27*(26), 6984–6994.
- Battaglini, L., Campana, G., & Casco, C. (2013). Illusory speed is retained in memory during invisible motion. *i-Perception, 4*(3), 180–191. doi: 10.1068/i0562
- Battaglini, L., & Casco, C. (2016). Contribution of visuospatial and motion-tracking to invisible motion. *Frontiers in Psychology, 7*(SEP), 1–10. doi: 10.3389/fpsyg.2016.01369
- Becker, M. W., & Rasmussen, I. P. (2007). The rhythm aftereffect: Support for time sensitive neurons with broad overlapping tuning curves. *Brain and Cognition, 64*(3), 274–281. doi: 10.1016/j.bandc.2007.03.009
- Binda, P., Cicchini, G. M., Burr, D. C., & Morrone, M. C. (2009). Spatiotemporal Distortions of Visual Perception at the Time of Saccades. *Journal of Neuroscience, 29*(42), 13147–13157. doi: 10.1523/JNEUROSCI.3723-09.2009
- Binetti, N., Hagura, N., Fadipe, C., Tomassini, A., Walsh, V., & Bestmann, S. (2015).



- Binding space and time through action. *Proceedings of the royal society*, 22–27. doi: 10.5061/dryad.73fq4
- Bizo, L. A., Chu, J. Y., Sanabria, F., & Killeen, P. R. (2006). The failure of weber's law in time perception and production. *Behavioural Processes*, 71(2-3), 201–210.
- Blakemore, S.-J., Wolpert, D., & Frith, C. (2000). Why can't you tickle yourself? *Neuroreport*, 11(11), R11–R16.
- Block, R. A. (1978). Remembered duration: Effects of event and sequence complexity. *Memory & Cognition*, 6(3), 320–326.
- Block, R. A., & Gruber, R. P. (2014). Time perception, attention, and memory: a selective review. *Acta psychologica*, 149, 129–133.
- Block, R. A., & Zakay, D. (1997). Prospective and retrospective duration judgments: A meta-analytic review. *Psychonomic Bulletin and Review*, 4(2), 184–197. doi: 10.3758/BF03209393
- Block, R. A., & Zakay, D. (2004). Prospective and retrospective duration judgments: an executive-control process. *Acta Neurobiologiae Experimentalis*, 64, 319–328.
- Boltz, M. G. (2005). Duration judgments of naturalistic events in the auditory and visual modalities. *Perception and Psychophysics*, 67(8), 1362–1375. doi: 10.3758/BF03193641
- Braddick, O. (1974). A short-range process in apparent motion. *Vision Research*, 14(7), 519–527. doi: 10.1016/0042-6989(74)90041-8
- Braddick, O. J. (1980). Low-level and high-level processes in apparent motion. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 290(1038), 137–151. doi: 10.1098/rstb.1980.0087
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10(4), 433–436. doi: 10.1163/156856897X00357
- Brand, A., Urban, A., & Grothe, B. (2000). Duration Tuning in the Mouse Auditory Midbrain ANTJE. *Journal of Neurophysiology*, 84(4), 1790–1799. doi: 10.1523/JNEUROSCI.1964-09.2010
- Brenner, E., & Smeets, J. B. (2010). How well can people judge when something happened? *Vision Research*, 50(12), 1101–1108.
- Brenner, E., & Smeets, J. B. (2015). How people achieve their amazing temporal precision in interception. *Journal of Vision*, 15(3), 8–8.
- Brown. (1985). Time perception and attention: The effects of prospective versus retrospective paradigms and task demands on perceived duration. *Perception & Psychophysics*, 38(2), 115–124.
- Brown, P., Rothwell, J. C., & Marsden, C. D. (1997). The stiff leg syndrome. *Journal of Neurology Neurosurgery and Psychiatry*, 62(1), 31–37. doi: 10.1136/jnnp.62.1.31
- Bruno, A., Ayhan, I., & Johnston, A. (2010). Retinotopic adaptation-based visual

- duration compression. *Journal of Vision*, 10(10), 30–30. doi: 10.1167/10.10.30
- Bruno, A., Ayhan, I., & Johnston, A. (2011). Duration expansion at low luminance levels. *Journal of Vision*, 11(14), 13–13. doi: 10.1167/11.14.13
- Bruno, N. (2001). When does action resist visual illusions? *Trends in Cognitive Sciences*, 5(9), 379–382.
- Bryce, D., & Bratzke, D. (2016). Multiple timing of nested intervals: Further evidence for a weighted sum of segments account. *Psychonomic Bulletin and Review*, 23(1), 317–323. doi: 10.3758/s13423-015-0877-5
- Bueti, D., & Buonomano, D. V. (2014). Temporal perceptual learning. *Timing and Time Perception*, 2(3), 261–289. doi: 10.1163/22134468-00002023
- Bueti, D., Lasaponara, S., Cercignani, M., & Macaluso, E. (2012). Learning about Time: Plastic Changes and Interindividual Brain Differences. *Neuron*, 75(4), 725–737. doi: 10.1016/j.neuron.2012.07.019
- Bueti, D., Walsh, V., Frith, C., & Rees, G. (2008). Different Brain Circuits Underlie Motor and Perceptual Representations of Temporal Intervals. *Journal of Cognitive Neuroscience*, 204–214.
- Buhusi, C. V., & Meck, W. H. (2005). What makes us tick? Functional and neural mechanisms of interval timing. *Nature Reviews Neuroscience*, 6(10), 755–765. doi: 10.1038/nrn1764
- Buonomano, D. V. (2000). Decoding temporal information: a model based on short-term synaptic plasticity. *Journal of Neuroscience*, 20(3), 1129–1141.
- Buonomano, D. V., Bramen, J., & Khodadadifar, M. (2009). Influence of the interstimulus interval on temporal processing and learning: Testing the state-dependent network model. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1525), 1865–1873. doi: 10.1098/rstb.2009.0019
- Buonomano, D. V., & Karmarkar, U. R. (2002). Review: How Do We Tell Time? *The Neuroscientist*, 8(1), 42–51. doi: 10.1177/107385840200800109
- Buonomano, D. V., & Laje, R. (2011). Population Clocks: Motor Timing with Neural Dynamics. *Space, Time and Number in the Brain*, 14(12), 71–85. doi: 10.1016/B978-0-12-385948-8.00006-2
- Burr, D., Banks, M. S., & Morrone, M. C. (2009). Auditory dominance over vision in the perception of interval duration. *Experimental Brain Research*, 198(1), 49–57. doi: 10.1007/s00221-009-1933-z
- Burr, D., Della Rocca, E., & Morrone, M. C. (2013). Contextual effects in interval-duration judgements in vision, audition and touch. *Experimental Brain Research*, 230(1), 87–98.
- Burr, D., Tozzi, A., & Morrone, M. C. (2007). Neural mechanisms for timing visual events are spatially selective in real-world coordinates. *Nature Neuroscience*,

- 10(4), 423–425. doi: 10.1038/nn1874
- Buzsáki, G. (2010). Neural Syntax: Cell Assemblies, Synapsesembles, and Readers. *Neuron*, 68(3), 362–385. doi: 10.1016/j.neuron.2010.09.023
- Cameron, B. D., & López-Moliner, J. (2015). Target modality affects visually guided online control of reaching. *Vision Research*, 110, 233–243.
- Cardoso-Leite, P., & Gorea, A. (2009). Comparison of Perceptual and Motor Decisions Via Confidence Judgments and Saccade Curvature. *Journal of Neurophysiology*, 101(6), 2822–2836. doi: 10.1152/jn.91269.2008
- Cardoso-Leite, P., Gorea, A., & Mamassian, P. (2007). Temporal order judgment and simple reaction times. *Journal of Vision*, 7(6), 1–14. doi: 10.1167/7.6.11
- .Introduction
- Cardoso-Leite, P., Mamassian, P., Schütz-Bosbach, S., & Waszak, F. (2010). A new look at sensory attenuation: Action-effect anticipation affects sensitivity, not response bias. *Psychological Science*, 21(12), 1740–1745. doi: 10.1177/0956797610389187
- Carlson, T. A., Hogendoorn, H., & Verstraten, F. A. J. (2006). The speed of visual attention: What time is it? *Journal of Vision*, 6(12), 6. doi: 10.1167/6.12.6
- Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, 51(13), 1484–1525.
- Carrasco, M., Giordano, A. M., & McElree, B. (2004). Temporal performance fields: Visual and attentional factors. *Vision Research*, 44(12), 1351–1365.
- Carrasco, M., Giordano, A. M., & McElree, B. (2006). Attention speeds processing across eccentricity: Feature and conjunction searches. *Vision Research*, 46(13), 2028–2040.
- Carrasco, M., McElree, B., Denisova, K., & Giordano, A. M. (2003). Speed of visual processing increases with eccentricity. *Nature Neuroscience*, 6(7), 699.
- Casseday, J. H., Ehrlich, D., & Covey, E. (1994). Neural tuning for sound duration: Role of inhibitory mechanisms in the inferior colliculus. *Science*, 264(5160), 847–850. doi: 10.1126/science.8171341
- Cecere, R., Rees, G., & Romei, V. (2015). Individual differences in alpha frequency drive crossmodal illusory perception. *Current Biology*, 25(2), 231–235. doi: 10.1016/j.cub.2014.11.034
- Chang, C.-J., & Jazayeri, M. (2018). Integration of speed and time for estimating time to contact. *Proceedings of the National Academy of Sciences*, 115(12), 201713316. doi: 10.1073/pnas.1713316115
- Cheng, X., Yang, Q., Han, Y., Ding, X., & Fan, Z. (2014). Capacity limit of simultaneous temporal processing: How many concurrent ‘clocks’ in vision? *PLoS ONE*, 9(3). doi: 10.1371/journal.pone.0091797

- Chien, S.-e., Ono, F., & Watanabe, K. (2011). Mislocalization of Visual Stimuli: Independent Effects of Static and Dynamic Attention. *PLoS ONE*, *6*(12), e28371. doi: 10.1371/journal.pone.0028371
- Chow, A., Gozli, D. G., & Pratt, J. (2014). Examining the locus of the attentional attraction effect. *Attention, Perception, and Psychophysics*, *76*(8), 2389–2397. doi: 10.3758/s13414-014-0724-1
- Church, R. M. (1984). Properties of the Internal Clock. *Annals of the New York Academy of Sciences*, *423*(1), 566–582. doi: 10.1111/j.1749-6632.1984.tb23459.x
- Cleland, B., Levick, W., & Sanderson, K. (1973). Properties of sustained and transient ganglion cells in the cat retina. *The Journal of Physiology*, *228*(3), 649–680.
- Clifford, C., Arnold, D., & Pearson, J. (2003). A paradox of temporal perception revealed by a stimulus oscillating in colour and orientation. *Vision Research*, *43*(21), 2245–2253. doi: 10.1016/S0042-6989(03)00120-2
- Clifford, C., Spehar, B., & Pearson, J. (2004). Motion transparency promotes synchronous perceptual binding. *Vision Research*, *44*(26), 3073–3080. doi: 10.1016/j.visres.2004.07.022
- Cohen, J., Hansel, C., & Sylvester, J. D. (1953). A new phenomenon in time judgment. *Nature*, *172*(4385), 901.
- Cos, I., Belanger, N., & Cisek, P. (2011). The influence of predicted arm biomechanics on decision making. *Journal of Neurophysiology*, *105*(6), 3022–3033. doi: 10.1152/jn.00975.2010
- Cos, I., Duque, J., & Cisek, P. (2014). Rapid prediction of biomechanical costs during action decisions. *Journal of Neurophysiology*, *112*(6), 1256–1266. doi: 10.1152/jn.00147.2014
- Cos, I., Medleg, F., & Cisek, P. (2012). The modulatory influence of end-point controllability on decisions between actions. *Journal of Neurophysiology*, *108*(6), 1764–1780. doi: 10.1152/jn.00081.2012
- Coull, J. T., Vidal, F., Nazarian, B., & Macar, F. (2004). Functional anatomy of the attentional modulation of time estimation. *Science*, *303*(5663), 1506–1508.
- Cravo, A. M., Rohenkohl, G., Wyart, V., & Nobre, A. C. (2011). Endogenous modulation of low frequency oscillations by temporal expectations. *Journal of Neurophysiology*, *106*(6), 2964–2972. doi: 10.1152/jn.00157.2011
- Creelman, C. D. (1962). Human Discrimination of Auditory Duration. *The Journal of the Acoustical Society of America*, *34*(5), 582–593. doi: 10.1121/1.1918172
- Curran, W., Benton, C., Harris, J., Hibbard, P., & Lee, B. (2016). Adapting to time: Duration channels do not mediate human time perception. *Journal of Vision*, *16*(5), 1–10. doi: 10.1167/16.5.4.doi
- Danquah, A. N., Farrell, M. J., & O'Boyle, D. J. (2008). Biases in the subjective

- timing of perceptual events: Libet et al. (1983) revisited. *Consciousness and Cognition*, 17(3), 616–627. doi: 10.1016/j.concog.2007.09.005
- De Freitas, J., Myers, N. E., & Nobre, A. C. (2016). Tracking the changing feature of a moving object. *Journal of Vision*, 16(3), 22. doi: 10.1167/16.3.22
- Dean, M., Wu, S.-W., & Maloney, L. T. (2007). Trading off speed and accuracy in rapid, goal-directed movements. *Journal of Vision*, 7(5), 10. doi: 10.1167/7.5.10
- de Gardelle, V., & Mamassian, P. (2014). Does confidence use a common currency across two visual tasks? *Psychological Science*, 25(6), 1286–1288. doi: 10.1177/0956797614528956
- de Montalembert, M., & Mamassian, P. (2012). Processing temporal events simultaneously in healthy human adults and in hemi-neglect patients. *Neuropsychologia*, 50(5), 791–799. doi: 10.1016/j.neuropsychologia.2012.01.013
- Di Luca, M., Machulla, T. K., & Ernst, M. O. (2009). Recalibration of multisensory simultaneity: Cross-modal transfer coincides with a change in perceptual latency. *Journal of Vision*, 9(12), 7–7. doi: 10.1167/9.12.7
- Droit-Volet, S. (2010). Stop using time reproduction tasks in a comparative perspective without further analyses of the role of the motor response: The example of children. *European Journal of Cognitive Psychology*, 22(1), 130–148. doi: 10.1080/09541440902738900
- Droit-Volet, S., & Meck, W. H. (2007). How emotions colour our perception of time. *Trends in Cognitive Sciences*, 11(12), 504–513. doi: 10.1016/j.tics.2007.09.008
- Duncan, R. O., & Boynton, G. M. (2003). Cortical magnification within human primary visual cortex correlates with acuity thresholds. *Neuron*, 38(4), 659–671.
- Duyck, M., Collins, T., & Wexler, M. (2015). Does time stop when we blink? *Journal of Vision*, 15(12), 370–370.
- Eagleman, D. M. (2008). Human time perception and its illusions. *Current Opinion in Neurobiology*, 18(2), 131–136. doi: 10.1016/j.conb.2008.06.002.Human
- Ehrlich, D., Casseday, J. H., & Covey, E. (1997). Neural tuning to sound duration in the inferior colliculus of the big brown bat, *Eptesicus fuscus*. *Journal of neurophysiology*, 77(5), 2360–2372. doi: 10.1152/jn.1997.77.5.2360
- Eichenbaum, H. (2015). Time cells in the hippocampus: a new dimension for mapping memories. *Nature Reviews Neuroscience*, 15(11), 732–744. doi: 10.1038/nrn3827.Time
- Eijkman, E., & Vendrik, A. J. H. (1965). Can a Sensory System be Specified by Its Internal Noise? *The Journal of the Acoustical Society of America*, 37(6), 1102–1109. doi: 10.1121/1.1909530

- Elliott, D., Helsen, W. F., & Chua, R. (2001). A century later: Woodworth's (1899) two-component model of goal-directed aiming. *Psychological Bulletin*, *127*(3), 342.
- Engelbrecht, S. E. (2001). Minimum Principles in Motor Control. *Journal of Mathematical Psychology*, *45*(3), 497–542. doi: 10.1006/jmps.2000.1295
- Eriksson, D., Tompa, T., & Roland, P. E. (2008). Non-linear population firing rates and voltage sensitive dye signals in visual areas 17 and 18 to short duration stimuli. *PLoS ONE*, *3*(7). doi: 10.1371/journal.pone.0002673
- Ernst, M. O. (2006). A Bayesian view on multimodal cue integration. In G. Knoblich, I. M. Thornton, M. Grosjean, & M. Shiffrar (Eds.), *Human body perception from the inside out*. publisher.
- Ernst, M. O. (2007). Learning to combine arbitrary signals from vision and touch. *Journal of Vision*, *7*(5), 1–14. doi: 10.1167/7.5.7
- Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, *415*(6870), 429–433. doi: 10.1038/415429a
- Faisal, A. A., & Wolpert, D. M. (2009). Near optimal combination of sensory and motor uncertainty in time during a naturalistic perception-action task. *Journal of Neurophysiology*, *101*(4), 1901–1912.
- Fendrich, R., & Corballis, P. M. (2001). The temporal cross-capture of audition and vision. *Perception and Psychophysics*, *63*(4), 719–725. doi: 10.3758/BF03194432
- Fitts, P. M. (1954). The Information Capacity of the Human Motor. *Journal of Experimental Biology*, *47*(6), 381–391. doi: 10.1037/h0055392
- Fleming, S. M., Maniscalco, B., Ko, Y., Amendi, N., Ro, T., & Lau, H. (2015). Action-Specific Disruption of Perceptual Confidence. *Psychological Science*, *26*(1), 89–98. doi: 10.1177/0956797614557697
- Forte, J., Hogben, J. H., & Ross, J. (1999). Spatial limitations of temporal segmentation. *Vision Research*, *39*(24), 4052–4061. doi: 10.1016/S0042-6989(99)00124-8
- Fox, J., Friendly, G. G., Graves, S., Heiberger, R., Monette, G., Nilsson, H., . . . Suggets, M. (2007). The car package. *R Foundation for Statistical Computing*.
- Fraisse, P. (1963). *The psychology of time*. Harper & Row.
- Fraisse, P. (1984). Perception and estimation of time. *Annual Review of Psychology*, *35*(1), 1–37.
- Franz, V. H. (2001). Action does not resist visual illusions. *Trends in Cognitive Sciences*, *5*(11), 457–459.
- Franz, V. H., Gegenfurtner, K. R., Bühlhoff, H. H., & Fahle, M. (2000). Grasping visual illusions: No evidence for a dissociation between perception and action. *Psychological Science*, *11*(1), 20–25.

- French, R. M., Addyman, C., Mareschal, D., & Thomas, E. (2014). GAMIT – A Fading-Gaussian Activation Model of Interval-Timing: Unifying Prospective and Retrospective Time Estimation. *Timing & Time Perception Reviews*, 1(December), 1–17. doi: 10.1016/j.sbspro.2014.02.348
- Freund, H.-J. (1986). Time control of hand movements. *Progress in Brain Research*, 64, 287–294. doi: [http://dx.doi.org/10.1016/S0079-6123\(08\)63423-8](http://dx.doi.org/10.1016/S0079-6123(08)63423-8)
- Fujisaki, W., Koene, A., Arnold, D., Johnston, A., & Nishida, S. (2006). Visual search for a target changing in synchrony with an auditory signal. *Proceedings of the Royal Society B: Biological Sciences*, 273(1588), 865–874. doi: 10.1098/rspb.2005.3327
- Fujisaki, W., & Nishida, S. (2005). Temporal frequency characteristics of synchrony-asynchrony discrimination of audio-visual signals. *Experimental Brain Research*, 166(3-4), 455–464. doi: 10.1007/s00221-005-2385-8
- Fujisaki, W., & Nishida, S. (2010). A common perceptual temporal limit of binding synchronous inputs across different sensory attributes and modalities. *Proceedings of the Royal Society B: Biological Sciences*, 277(1692), 2281–2290. doi: 10.1098/rspb.2010.0243
- Fujisaki, W., Shimojo, S., Kashino, M., & Nishida, S. (2004). Recalibration of audio-visual simultaneity. *Nature Neuroscience*, 7(7), 773–778. doi: 10.1038/nn1268
- Fukuda, Y., & Stone, J. (1974). Retinal distribution and central projections of y-, x-, and w-cells of the cat's retina. *Journal of Neurophysiology*, 37(4), 749–772.
- Fulcher, C., Heron, J., McGraw, P. V., Roach, N. W., & Whitaker, D. (2016). Object size determines the spatial spread of visual time. *Proceedings of the Royal Society B*(8). doi: 10.1098/rspb.2016.1024
- Gallistel, C. R. (2011). Mental Magnitudes. *Space, Time and Number in the Brain*, 3–12. doi: 10.1016/B978-0-12-385948-8.00001-3
- Gallistel, C. R., & Gibbon, J. (2000). Time, rate, and conditioning. *Psychological Review*, 107(2), 289–344. doi: 10.1037/0033-295X.107.2.289
- García-Pérez, M. A., & Alcalá-Quintana, R. (2012). On the discrepant results in synchrony judgment and temporal-order judgment tasks: A quantitative model. *Psychonomic Bulletin and Review*, 19(5), 820–846. doi: 10.3758/s13423-012-0278-y
- García-Pérez, M. A., & Alcalá-Quintana, R. (2017). Perceived temporal order and simultaneity: Beyond psychometric functions. In A. Vatakis, F. Balci, M. Di Luca, & A. Correa (Eds.), *Timing and time perception: Procedures, measures, and applicationt*. Brill.
- Gepshtein, S., & Banks, M. (2003). Viewing Geometry Determines How Vision and Haptics Combine in Size Perception. *Current Biology*, 13(2), 483–488. doi:

- 10.1016/S
- Ghose, G. M., Yang, T., & Maunsell, J. H. R. (2002). Physiological Correlates of Perceptual Learning in Monkey V1 and V2. *Journal of Neurophysiology*, *87*(4), 1867–1888. doi: 10.1152/jn.00690.2001
- Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological Review*, *84*(3), 279–325. doi: 10.1037/0033-295X.84.3.279
- Gibbon, J., Church, R. M., & Meck, W. H. (1984). Scalar timing in memory. *Annals of the New York Academy of Sciences*, *423*(1), 52–77.
- Gibbon, J., & Rutschmann, R. (1969). Temporal Order Judgment and Reaction Time. *Science*, *165*, 413–415.
- Giersch, A., Poncelet, P. E., Capa, R. L., Martin, B., Duval, C. Z., Curziotti, M., ... Lalanne, L. (2015). Disruption of information processing in schizophrenia: The time perspective. *Schizophrenia Research: Cognition*, *2*(2), 78–83. doi: 10.1016/j.scog.2015.04.002
- Giraud, A. L., & Poeppel, D. (2012). Cortical oscillations and speech processing: Emerging computational principles and operations. *Nature Neuroscience*, *15*(4), 511–517. doi: 10.1038/nn.3063
- Goodale, M. A., & Humphrey, G. K. (1998). The objects of action and perception. *Cognition*, *67*(1-2), 181–207.
- Gorea, A. (2011). Ticks per thought or thoughts per tick? A selective review of time perception with hints on future research. *Journal of Physiology Paris*, *105*(4-6), 153–163. doi: 10.1016/j.jphysparis.2011.09.008
- Gorgoraptis, N., Catalao, R. F. G., Bays, P. M., & Husain, M. (2011). Dynamic Updating of Working Memory Resources for Visual Objects. *Journal of Neuroscience*, *31*(23), 8502–8511. doi: 10.1523/JNEUROSCI.0208-11.2011
- Grabot, L., Kosem, A., Azizi, L., & van Wassenhove, V. (2017). Prestimulus Alpha Oscillations and the Temporal Sequencing of Audiovisual Events. *Journal of Cognitive Neuroscience*, *29*(9), 1566–1582. doi: 10.1162/jocn
- Graf, E. W., Warren, P. A., & Maloney, L. T. (2005). Explicit estimation of visual uncertainty in human motion processing. *Vision Research*, *45*(24), 3050–3059. doi: 10.1016/j.visres.2005.08.007
- Grondin, S. (2010). Timing and time perception: a review of recent behavioral and neuroscience findings and theoretical directions. *Attention, Perception, & Psychophysics*, *72*(3), 561–582.
- Grondin, S. (2012). Violation of the scalar property for time perception between 1 and 2 seconds: evidence from interval discrimination, reproduction, and categorization. *Journal of Experimental Psychology: Human Perception and Performance*, *38*(4), 880.



- Gu, B.-m., Rijn, H. V., & Meck, W. H. (2015). Neuroscience and Biobehavioral Reviews Oscillatory multiplexing of neural population codes for interval timing and working memory. *Neuroscience and Biobehavioral Reviews*, *48*, 160–185. doi: 10.1016/j.neubiorev.2014.10.008
- Hanson, J. V., Heron, J., & Whitaker, D. (2008). Recalibration of perceived time across sensory modalities. *Experimental Brain Research*, *185*(2), 347–352. doi: 10.1007/s00221-008-1282-3
- Harrar, V., & Harris, L. R. (2005). Simultaneity constancy: detecting events with touch and vision. *Experimental Brain Research*, *166*(3-4), 465–473.
- Harrar, V., & Harris, L. R. (2008). The effect of exposure to asynchronous audio, visual, and tactile stimulus combinations on the perception of simultaneity. *Experimental Brain Research*, *186*(4), 517–524. doi: 10.1007/s00221-007-1253-0
- Hartcher-O'Brien, J., & Alais, D. (2011). Temporal Ventriloquism in a Purely Temporal Context. *Journal of Experimental Psychology: Human Perception and Performance*, *37*(5), 1383–1395. doi: 10.1037/a0024234
- Hayashi, M. J., Ditye, T., Harada, T., Hashiguchi, M., Sadato, N., Carlson, S., ... Kanai, R. (2015). Time Adaptation Shows Duration Selectivity in the Human Parietal Cortex. *PLoS Biology*, *13*(9), 1–27. doi: 10.1371/journal.pbio.1002262
- Hayashi, M. J., Kantele, M., Walsh, V., Carlson, S., & Kanai, R. (2014). Dissociable neuroanatomical correlates of subsecond and suprasedond time perception. *Journal of Cognitive Neuroscience*, *26*(8), 1685–1693. doi: 10.1162/jocn
- He, J., Hashikawa, T., Ojima, H., & Kinouchi, Y. (1997). Temporal integration and duration tuning in the dorsal zone of cat auditory cortex. *The Journal of Neuroscience*, *17*(7), 2615–2625.
- Heil, P., & Irvine, D. R. F. (1997). First-Spike Timing of Auditory-Nerve Fibers and Comparison With Auditory Cortex. *Journal of Neurophysiology*, *78*(5), 2438–2454. doi: 10.1152/jn.1997.78.5.2438
- Henry, M. J., & McAuley, J. D. (2009). Evaluation of an Imputed Pitch Velocity Model of the Auditory Kappa Effect. *Journal of Experimental Psychology: Human Perception and Performance*, *35*(2), 551–564. doi: 10.1037/0096-1523.35.2.551
- Heron, J., Aaen-Stockdale, C., Hotchkiss, J., Roach, N. W., McGraw, P. V., & Whitaker, D. (2012). Duration channels mediate human time perception. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1729), 690–698. doi: 10.1098/rspb.2011.1131
- Heron, J., Hotchkiss, J., Aaen-stockdale, C., Roach, N. W., & Whitaker, D. (2013). A neural hierarchy for illusions of time : Duration adaptation precedes multisensory integration. *Journal of Vision*, *13*(14), 1–12. doi: 10.1167/13.14.4

- Heron, J., Roach, N. W., Hanson, J. V., McGraw, P. V., & Whitaker, D. (2012). Audio-visual time perception is spatially specific. *Experimental Brain Research*, *218*(3), 477–485. doi: 10.1007/s00221-012-3038-3
- Herrmann, C. S., Murray, M. M., Ionta, S., Hutt, A., & Lefebvre, J. (2016). Shaping Intrinsic Neural Oscillations with Periodic Stimulation. *The Journal of Neuroscience*, *36*(19), 5328–5337. doi: 10.1523/JNEUROSCI.0236-16.2016
- Hess, R. F., & Fredericksen, R. E. (2002). Temporal detection in human vision: Dependence on eccentricity. *Ophthalmic and Physiological Optics*, *22*(2), 92–102. doi: 10.1046/j.1475-1313.2002.00011.x
- Hess, R. F., & Maehara, G. (2011). Does cognitive perception have access to brief temporal events? *i-Perception*, *2*(2), 142–149. doi: 10.1068/i0418
- Heusser, A. C., Poeppel, D., Ezzyat, Y., & Davachi, L. (2017). Episodic sequence memory is supported by a theta-gamma phase code. *Nature Neuroscience*, *19*(10), 1374–1380. doi: 10.1038/nn.4374.Episodic
- Hillis, J. M., Ernst, M. O., Banks, M. S., & Landy, M. S. (2002a). Combining Sensory Information: Mandatory Fusion Within, but Not Between, Senses. *Science*, *1627*(2002), 1–4. doi: 10.1126/science.1075396
- Hillis, J. M., Ernst, M. O., Banks, M. S., & Landy, M. S. (2002b). Combining sensory information: mandatory fusion within, but not between, senses. *Science*, *298*(5598), 1627–1630.
- Hillis, J. M., Watt, S. J., Landy, M. S., & Banks, M. S. (2004). Slant from texture and disparity cues: Optimal cue combination. *Journal of Vision*, *4*(12), 1. doi: 10.1167/4.12.1
- Hirsh, I. J., & Sherrick, C. E. (1961). Perceived order in different sense modalities. *Journal of Experimental Psychology*, *62*(5), 423–432. doi: 10.1037/h0045283
- Hodinott-Hill, I., Thilo, K. V., Cowey, A., & Walsh, V. (2002). Auditory chronostasis: Hanging on the telephone. *Current Biology*, *12*(20), 1779–1781. doi: 10.1016/S0960-9822(02)01219-8
- Hogendoorn, H., Carlson, T. A., VanRullen, R., & Verstraten, F. A. (2010). Timing divided attention. *Attention, perception & psychophysics*, *72*(8), 2059–2068. doi: 10.3758/APP
- Holcombe, A. O. (2009). Seeing slow and seeing fast: two limits on perception. *Trends in Cognitive Sciences*, *13*(5), 216–221. doi: 10.1016/j.tics.2009.02.005
- Holcombe, A. O., & Cavanagh, P. (2008). Independent, synchronous access to color and motion features. *Cognition*, *107*(2), 552–580. doi: 10.1016/j.cognition.2007.11.006
- Hommel, B. (2011). The Simon effect as tool and heuristic. *Acta Psychologica*, *136*(2), 189–202. doi: 10.1016/j.actpsy.2010.04.011

- Hothorn, T., Bretz, F., Westfall, P., Heiberger, R. M., Schuetzenmeister, A., Scheibe, S., & Hothorn, M. T. (2017). Package 'multcomp'. <http://cran.r-project.org/web/packages/multcomp/multcomp>.
- Hudson, T. E., Maloney, L. T., & Landy, M. S. (2008). Optimal compensation for temporal uncertainty in movement planning. *PLoS Computational Biology*, 4(7). doi: 10.1371/journal.pcbi.1000130
- Ivry, R. B. (1996). The representation of temporal information in perception and motor control. *Current Opinion in Neurobiology*, 6(6), 851–857. doi: 10.1016/S0959-4388(96)80037-7
- Ivry, R. B., & Hazeltine, E. (1995). Perception and production of temporal intervals across a range of duration. [CD-ROM]. *Journal of Experimental Psychology*, 21(1), 3–18.
- Ivry, R. B., & Spencer, R. M. (2004). The neural representation of time. *Current Opinion in Neurobiology*, 14(2), 225–232. doi: 10.1016/j.conb.2004.03.013
- Jarosz, A. F., & Wiley, J. (2014). What Are the Odds? A Practical Guide to Computing and Reporting Bayes Factors. *The Journal of Problem Solving*, 7(1), 2–9. doi: 10.7771/1932-6246.1167
- Jarvstad, A., Hahn, U., Warren, P. A., & Rushton, S. K. (2014). Are perceptuo-motor decisions really more optimal than cognitive decisions? *Cognition*, 130(3), 397–416. doi: 10.1016/j.cognition.2013.09.009
- Jaskowski, P. (1996). Simple Reaction Time and Perception of Temporal Order: Dissociations and Hypotheses. *Perceptual and Motor Skills*, 82(3), 707–730. doi: 10.2466/pms.1996.82.3.707
- Jaśkowski, P., Jaroszyk, F., & Hojan-Jezińska, D. (1990). Temporal-order judgments and reaction time for stimuli of different modalities. *Psychological Research*, 52(1), 35–38. doi: 10.1007/BF00867209
- Jazayeri, M., & Shadlen, M. N. (2010). Temporal context calibrates interval timing. *Nature Neuroscience*, 13(8), 1020–1026. doi: 10.1038/nn.2590
- Johnston, A. (2010). Modulation of time perception by visual adaptation. In A. Nobre & J. Coull (Eds.), *Attention and time* (pp. 187–200). Oxford University Press Oxford.
- Johnston, A., Arnold, D. H., & Nishida, S. (2006). Spatially localized distortions of event time. *Current Biology*, 16(5), 472–479. doi: 10.1016/j.cub.2006.01.032
- Johnston, A., Bruno, A., Watanabe, J., Quansah, B., Patel, N., Dakin, S., & Nishida, S. (2008). Visually-based temporal distortion in dyslexia. *Vision Research*, 48(17), 1852–1858.
- Johnston, A., & Clifford, C. (1995). A unified account of three apparent motion illusions. *Vision Research*, 35(8), 1109–1124.

- Johnston, A., & Nishida, S. (2001). Time perception: Brain time or event time? *Current Biology*, *11*(11), 427–430. doi: 10.1016/S0960-9822(01)00252-4
- Jonikaitis, D., Deubel, H., & De'Sperati, C. (2009). Time gaps in mental imagery introduced by competing saccadic tasks. *Vision Research*, *49*(17), 2164–2175. doi: 10.1016/j.visres.2009.05.021
- Kanai, R., Paffen, C. L., Gerbino, W., & Verstraten, F. A. (2004). Blindness to inconsistent local signals in motion transparency from oscillating dots. *Vision Research*, *44*(19), 2207–2212. doi: 10.1016/j.visres.2004.04.010
- Kanai, R., Paffen, C. L., Hogendoorn, H., & Verstraten, F. A. (n.d.). Time dilation in dynamic visual display. *Journal of Vision*, *6*.
- Kaneko, S., & Murakami, I. (2009). Perceived duration of visual motion increases with speed. *Journal of Vision*, *9*(7), 14–14.
- Karmarkar, U. R., & Buonomano, D. V. (2007a). Timing in the Absence of Clocks: Encoding Time in Neural Network States. *Neuron*, *53*(3), 427–438. doi: 10.1016/j.neuron.2007.01.006
- Karmarkar, U. R., & Buonomano, D. V. (2007b). Timing in the Absence of Clocks: Encoding Time in Neural Network States. *Neuron*, *53*(3), 427–438. doi: 10.1016/j.neuron.2007.01.006
- Keele, S. W., Pokorny, R. A., Corcos, D. M., & Ivry, R. (1985). Do perception and motor production share common timing mechanisms: A correlational analysis. *Acta Psychologica*, *60*(2-3), 173–191. doi: 10.1016/0001-6918(85)90054-X
- Keetels, M., & Vroomen, J. (2005). The role of spatial disparity and hemifields in audio-visual temporal order judgments. *Experimental Brain Research*, *167*(4), 635–640. doi: 10.1007/s00221-005-0067-1
- Keetels, M., & Vroomen, J. (2008). Tactile-visual temporal ventriloquism: No effect of spatial disparity. *Perception and Psychophysics*, *70*(5), 765–771. doi: 10.3758/PP.70.5.765
- Kepecs, A., Uchida, N., Zariwala, H. A., & Mainen, Z. F. (2008). Neural correlates, computation and behavioural impact of decision confidence. *Nature*, *455*(7210), 227–231. doi: 10.1038/nature07200
- Khan, M. A., & Franks, I. M. (2003). Online versus offline processing of visual feedback in the production of component submovements. *Journal of Motor Behavior*, *35*(3), 285–295.
- Kiani, R., & Shadlen, M. N. (2009). Representation of confidence associated with a decision by neurons in the parietal cortex. *Science*, *324*(5928), 759–764.
- Klapproth, F. (2011). Temporal Decision Making in Simultaneous Timing. *Frontiers in Integrative Neuroscience*, *5*(October), 1–10. doi: 10.3389/fnint.2011.00071
- Klein, S. A., & Levi, D. M. (1987). Position sense of the peripheral retina. *Journal of*

- the Optical Society of America*, 4(8), 1543–1553. doi: 10.1364/JOSAA.5.000266
- Kleiner, M., Brainard, D. H., Pelli, D. G., Broussard, C., Wolf, T., & Niehorster, D. (2007). What's new in Psychtoolbox-3? *Perception*, 36, S14. doi: 10.1068/v070821
- Kliegl, K. M., & Huckauf, A. (2014). Perceived duration decreases with increasing eccentricity. *Acta Psychologica*, 150, 136–145. doi: 10.1016/j.actpsy.2014.05.007
- Klink, P. C., Montijn, J. S., & van Wezel, R. J. (2011). Crossmodal duration perception involves perceptual grouping, temporal ventriloquism, and variable internal clock rates. *Attention, Perception, and Psychophysics*, 73(1), 219–236. doi: 10.3758/s13414-010-0010-9
- Knill, D. C. (2003). Mixture models and the probabilistic structure of depth cues. *Vision Research*, 43(7), 831–854. doi: 10.1016/S0042-6989(03)00003-8
- Kononowicz, T. W., Roger, C., & van Wassenhove, V. (2017). Temporal metacognition as the decoding of self-generated brain dynamics. *bioRxiv*, 206086.
- Körding, K. P., Beierholm, U., Ma, W. J., Quartz, S., Tenenbaum, J. B., & Shams, L. (2007). Causal inference in multisensory perception. *PLoS ONE*, 2(9). doi: 10.1371/journal.pone.0000943
- Kösem, A., Gramfort, A., & Van Wassenhove, V. (2014). Encoding of event timing in the phase of neural oscillations. *NeuroImage*, 92, 274–284. doi: 10.1016/j.neuroimage.2014.02.010
- Krešević, J. L., Marinović, W., Johnston, A., & Arnold, D. H. (2016). Time order reversals and saccades. *Vision Research*, 125, 23–29. doi: 10.1016/j.visres.2016.04.005
- Kristofferson, A. (1967). Successiveness Discrimination as a Two-State, Quantal Process. *Science*, 158(October), 1337–1339.
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software*, 82(13).
- Landy, M. S., & Johnston, E. B. (1995). Measurement and Modeling of Depth Cue. *Vision research*, 35(3), 389–412. doi: 10.1016/0042-6989(94)00176-M
- Landy, M. S., & Kojima, H. (2001). Ideal cue combination for localizing texture-defined edges. *Journal of the Optical Society of America*, 18(9), 2307–2320. doi: 10.1364/JOSAA.18.002307
- Lebensfeld, P., & Wapner, S. (1968). Configuration and Space-Time Interdependence. *The American Journal of Psychology*, 81(1), 106–110.
- Lejeune, H., & Wearden, J. H. (2009a). Vierordt's the Experimental Study of the Time Sense (1868) and its legacy. *European Journal of Cognitive Psychology*, 21(6), 941–960. doi: 10.1080/09541440802453006

- Lejeune, H., & Wearden, J. H. (2009b). Vierordt's the experimental study of the time sense (1868) and its legacy. *European Journal of Cognitive Psychology*, *21*(6), 941–960.
- Levitan, C. A., Ban, Y. H. A., Stiles, N. R. B., & Shimojo, S. (2015). Rate perception adapts across the senses: Evidence for a unified timing mechanism. *Scientific Reports*, *5*(1), 1–6. doi: 10.1038/srep08857
- Lewis, P. A., & Miall, R. C. (2009). The precision of temporal judgement: Milliseconds, many minutes, and beyond. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1525), 1897–1905. doi: 10.1098/rstb.2009.0020
- Lewis, P. A., Miall, R. C., Daan, S., & Kacelnik, A. (2003). Interval timing in mice does not rely upon the circadian pacemaker. *Neuroscience Letters*, *348*(3), 131–134. doi: 10.1016/S0304-3940(03)00521-4
- Li, B., Yuan, X., & Huang, X. (2015). The aftereffect of perceived duration is contingent on auditory frequency but not visual orientation. *Scientific Reports*, *5*(March), 1–9. doi: 10.1038/srep10124
- Libet, B., Gleason, C. a., Wright, E. W., & Pearl, D. K. (1983). Time of Conscious Intention To Act in Relation To Onset of Cerebral Activity (Readiness-Potential). *Brain*, *106*(3), 623–642. doi: 10.1093/brain/106.3.623
- Linares, D., Cos, I., & Roseboom, W. (2016). Adaptation for multisensory relative timing. *Current Opinion in Behavioral Sciences*, *8*, 35–41. doi: 10.1016/j.cobeha.2016.01.005
- Linares, D., & Holcombe, A. O. (2014). Differences in perceptual latency estimated from judgments of temporal order, simultaneity and duration are inconsistent. *i-Perception*, *5*(6), 559–571. doi: 10.1068/i0675
- Linares, D., & López-Moliner, J. (2006). Perceptual asynchrony between color and motion with a single direction change. *Journal of Vision*, *6*(9), 10. doi: 10.1167/6.9.10
- Lisi, M., & Gorea, A. (2016). Time constancy in human perception. *Journal of Vision*, *16*(4), 1–12. doi: 10.1167/16.14.3.doi
- Lisman, J., & Jensen, O. (2013). The Theta-Gamma Neural Code. *Neuron*, *77*(6), 1002–1016. doi: 10.1016/j.neuron.2013.03.007.The
- Liverence, B. M., & Scholl, B. J. (2011). Selective attention warps spatial representation: Parallel but opposing effects on attended versus inhibited objects. *Psychological Science*, *22*(12), 1600–1608. doi: 10.1177/0956797611422543
- Locke, S. M., & Landy, M. S. (2017). Temporal causal inference with stochastic audiovisual sequences. *PLoS ONE*, *12*(9), 1–26. doi: 10.1371/journal.pone.0183776
- Loftus, G. R., & Masson, M. E. (1994). Using confidence intervals in within-subjects

- designs. *Psychon B Rev*, 1(4), 476–490. doi: 10.3758/BF03210951
- Love, S. A., Petrini, K., Cheng, A., & Pollick, F. E. (2013). A Psychophysical Investigation of Differences between Synchrony and Temporal Order Judgments. *PLoS ONE*, 8(1). doi: 10.1371/journal.pone.0054798
- Maarseveen, J., Hogendoorn, H., Verstraten, F. A., & Paffen, C. L. (2017). An investigation of the spatial selectivity of the duration after-effect. *Vision Research*, 130, 67–75. doi: 10.1016/j.visres.2016.11.003
- Macar, F., Grondin, S., & Casini, L. (1994). Controlled attention sharing influences time estimation. *Memory & Cognition*, 22(6), 673–686. doi: 10.3758/BF03209252
- MacKinnon, C. D., & Rothwell, J. C. (2000). Time-varying changes in corticospinal excitability accompanying the triphasic EMG pattern in humans. *Journal of Physiology*, 528(3), 633–645. doi: 10.1111/j.1469-7793.2000.00633.x
- Makin, A. D. J., Poliakoff, E., & El-Deredy, W. (2009). Tracking visible and occluded targets: Changes in event related potentials during motion extrapolation. *Neuropsychologia*, 47(4), 1128–1137. doi: 10.1016/j.neuropsychologia.2009.01.010
- Malapani, C., & Fairhurst, S. (2002). Scalar timing in animals and humans. *Learning and Motivation*, 33(1), 156–176. doi: 10.1006/lmot.2001.1105
- Maloney, L. T., & Zhang, H. (2010). Decision-theoretic models of visual perception and action. *Vision Research*, 50(23), 2362–2374. doi: 10.1016/j.visres.2010.09.031
- Mamassian, P. (2008). Overconfidence in an Objective Anticipatory Motor Task. *Psychological Science*, 19(6), 601–606.
- Mamassian, P. (2016). Visual confidence. *Annual review of vision science*, 2, 459–481.
- Mamassian, P., & Landy, M. S. (2010). It's that time again. *Nature Neuroscience*, 13(8), 914.
- Maniadakis, M., & Trahianias, P. (2016). When and how-long: A unified approach for time perception. *Frontiers in Psychology*, 7(MAR), 1–11. doi: 10.3389/fpsyg.2016.00466
- Masson, M. E. (2011). A tutorial on a practical Bayesian alternative to null-hypothesis significance testing. *Behavior Research Methods*, 43(3), 679–690. doi: 10.3758/s13428-010-0049-5
- Mastropasqua, T., Galliussi, J., Pascucci, D., & Turatto, M. (2015). Location transfer of perceptual learning: Passive stimulation and double training. *Vision Research*, 108, 93–102. doi: 10.1016/j.visres.2015.01.024
- Matell, M. S., King, G. R., & Meck, W. H. (2004). Differential Modulation of Clock

- Speed by the Administration of Intermittent Versus Continuous Cocaine. *Behavioral Neuroscience*, 118(1), 150–156. doi: 10.1037/0735-7044.118.1.150
- Matell, M. S., & Meck, W. H. (2004). Cortico-striatal circuits and interval timing: Coincidence detection of oscillatory processes. *Cognitive Brain Research*, 21(2), 139–170. doi: 10.1016/j.cogbrainres.2004.06.012
- Matthews, W. J., & Meck, W. H. (2014). Time perception: The bad news and the good. *Wiley Interdisciplinary Reviews: Cognitive Science*, 5(4), 429–446. doi: 10.1002/wcs.1298
- Mauk, M. D., & Buonomano, D. V. (2004). the Neural Basis of Temporal Processing. *Annual Review of Neuroscience*, 27(1), 307–340. doi: 10.1146/annurev.neuro.27.070203.144247
- McDonald, J. J., Teder-Sälejärvi, W. A., Heraldez, D., & Hillyard, S. A. (2001). Electrophysiological evidence for the "missing link" in crossmodal attention. *Canadian Journal of Experimental Psychology*, 55(2), 141–149. doi: 10.1037/h0087361
- McKee, S. P., & Taylor, D. G. (1984). Discrimination of time: comparison of foveal and peripheral sensitivity. *Journal of the Optical Society of America A, Optics and image science*, 1(6), 620–627. doi: 10.1364/JOSAA.1.000620
- McMains, S. A., & Somers, D. C. (2005). Processing efficiency of divided spatial attention mechanisms in human visual cortex. *Journal of Neuroscience*, 25(41), 9444–9448.
- Meck, W. H. (1996). Neuropharmacology of timing and time perception. *Cognitive Brain Research*, 3(3-4), 227–242. doi: 10.1016/0926-6410(96)00009-2
- Meck, W. H., & Ivry, R. B. (2016). Editorial overview: Time in perception and action. *Current Opinion in Behavioral Sciences*, 8, 6–10. doi: 10.1016/j.cobeha.2016.03.001
- Merchant, H., Zarco, W., Bartolo, R., & Prado, L. (2008). The context of temporal processing is represented in the multidimensional relationships between timing tasks. *PLoS ONE*, 3(9). doi: 10.1371/journal.pone.0003169
- Meredith, M. A., Nemitz, J. W., & Stein, B. E. (1987). Determinants of multisensory integration in superior colliculus neurons. I. Temporal factors. *The Journal of Neuroscience*, 7(10), 3215–29. doi: citeulike-article-id:409430
- Miall, C. (1989). The Storage of Time Intervals Using Oscillating Neurons. *Neural Computation*, 1(3), 359–371. doi: 10.1162/neco.1989.1.3.359
- Michon, J. a. (1990). Implicit and explicit representations of time. *Cognitive models of psychological time*, 37–58. doi: 10.1016/j.neunet.2009.01.008
- Mioni, G., Stablum, F., McClintock, S. M., & Grondin, S. (2014). Different methods for reproducing time, different results. *Attention, Perception, & Psychophysics*,



- 76(3), 675–681.
- Miyazaki, M., Kadota, H., Matsuzaki, K. S., Takeuchi, S., Sekiguchi, H., Aoyama, T., & Kochiyama, T. (2016). Dissociating the neural correlates of tactile temporal order and simultaneity judgements. *Scientific Reports*, 6(February), 1–10. doi: 10.1038/srep23323
- Miyazaki, M., Nozaki, D., & Nakajima, Y. (2005). Testing Bayesian Models of Human Coincidence Timing. *Journal of Neurophysiology*, 94(1), 395–399. doi: 10.1152/jn.01168.2004
- Morein-Zamir, S., Soto-Faraco, S., & Kingstone, A. (2003). Auditory capture of vision: Examining temporal ventriloquism. *Cognitive Brain Research*, 17(1), 154–163. doi: 10.1016/S0926-6410(03)00089-2
- Morey, R., Rouder, J., Jamil, T., Urbanek, S., Forner, K., & Ly, A. (2018). BayesFactor 0.9.12-4.2. *Comprehensive R Archive Network*.
- Morgan, M. J., Giora, E., & Solomon, J. A. (2008). A single "stopwatch" for duration estimation, a single "ruler" for size. *Journal of Vision*, 8(2), 14.1–8. doi: 10.1167/8.2.14
- Morrone, M. C., Ross, J., & Burr, D. (2005). Saccadic eye movements cause compression of time as well as space. *Nature Neuroscience*, 8(7), 950–954. doi: 10.1038/nn1488
- Motala, A., Heron, J., McGraw, P. V., Roach, N. W., & Whitaker, D. (2018). Rate after-effects fail to transfer cross-modally: Evidence for distributed sensory timing mechanisms. *Scientific Reports*, 8(1), 1–10. doi: 10.1038/s41598-018-19218-z
- Motoyoshi, I. (2004). The role of spatial interactions in perceptual synchrony. *Journal of Vision*, 4(5), 1–1. doi: 10.1167/4.5.1
- Moutoussis, K., & Zeki, S. (1997a). A direct demonstration of perceptual asynchrony in vision. *Proceedings of the Royal Society B: Biological Sciences*, 264(1380), 393–399. doi: 10.1098/rspb.1997.0056
- Moutoussis, K., & Zeki, S. (1997b). A direct demonstration of perceptual asynchrony in vision. *Proceedings of the Royal Society B: Biological Sciences*, 264(1380), 393–399. doi: 10.1098/rspb.1997.0056
- Moutoussis, K., & Zeki, S. (1997c). Functional segregation and temporal hierarchy of the visual perceptive systems. *Proceedings of the Royal Society B: Biological Sciences*, 264(1387), 1407–1414. doi: 10.1098/rspb.1997.0196
- Muller, T., & Nobre, A. C. (2014). Perceiving the passage of time: Neural possibilities. *Annals of the New York Academy of Sciences*, 1326(1), 60–71. doi: 10.1111/nyas.12545
- Nachmias, J. (2006). The role of virtual standards in visual discrimination. *Vision*

- Research*, 46(15), 2456–2464. doi: 10.1016/j.visres.2006.01.029
- Nagarajan, S. S., Blake, D. T., Wright, B. A., Byl, N., & Merzenich, M. M. (1998). Practice-related improvements in somatosensory interval discrimination are temporally specific but generalize across skin location, hemisphere, and modality. *The Journal of Neuroscience*, 18(4), 1559–1570.
- Nakajima, Y., Hoopen, G. T. E. N., Hilkhuisen, G., & Sasaki, T. (1992). Notes and Comment. *Perception & Psychophysics*, 51(5), 504–507. doi: 10.3758/BF03206102
- Nakajima, Y., Ten Hoopen, G., Hilkhuisen, G., & Sasaki, T. (1992). Time-shrinking: A discontinuity in the perception of auditory temporal patterns. *Perception & Psychophysics*, 51(5), 504–507.
- Navarra, J., García-Morera, J., & Spence, C. (2012). Temporal adaptation to audio-visual asynchrony generalizes across different sound frequencies. *Frontiers in Psychology*, 3(MAY), 1–7. doi: 10.3389/fpsyg.2012.00152
- Navarra, J., Hartcher-O'Brien, J., Piazza, E., & Spence, C. (2009). Adaptation to audiovisual asynchrony modulates the speeded detection of sound. *Proceedings of the National Academy of Sciences*, 106(23), 9169–9173.
- Navarra, J., Vatakis, A., Zampini, M., Soto-Faraco, S., Humphreys, W., & Spence, C. (2005). Exposure to asynchronous audiovisual speech extends the temporal window for audiovisual integration. *Cognitive Brain Research*, 25(2), 499–507. doi: 10.1016/j.cogbrainres.2005.07.009
- Nishida, S., & Johnston, A. (2002). Marker correspondence, not processing latency, determines temporal binding of visual attributes. *Current Biology*, 12(5), 359–368. doi: 10.1016/S0960-9822(02)00698-X
- Nishida, S., & Johnston, A. (2010). The time marker account of cross-channel temporal judgments. In R. Nijhawan & B. Khurana (Eds.), *Space and time in perception and action* (pp. 278–300). Cambridge University Press Cambridge, UK.
- Nobre, K., & Coull, J. (2010). *Attention and time*. Oxford University Press, USA.
- Olson, I. R., Gatenby, J. C., Leung, H. C., Skudlarski, P., & Gore, J. C. (2004). Neuronal representation of occluded objects in the human brain. *Neuropsychologia*, 42(1), 95–104. doi: 10.1016/S0028-3932(03)00151-9
- Ono, F., & Watanabe, K. (2011). Attention Can Retrospectively Distort Visual Space. *Psychological Science*, 22(4), 472–477. doi: 10.1177/0956797611403319
- Oprisan, S., & Buhusi, C. (2011). Modeling Pharmacological Clock and Memory Patterns of Interval Timing in a Striatal Beat-Frequency Model with Realistic, Noisy Neurons. *Frontiers in Integrative Neuroscience*, 5(September), 1–11. doi: 10.3389/fnint.2011.00052
- Oprisan, S., & Buhusi, C. (2014). What is all the noise about in interval timing?

- Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 14(Suppl 1), 3–5. doi: 10.1186/1471-2202-14-S1-P44
- Osaka, N. (1976). Reaction time as a function of peripheral retinal locus around fovea: Effect of stimulus size. *Perceptual and Motor Skills*, 43(2), 603–606. doi: 10.2466/pms.1976.43.2.603
- Pariyadath, V., & Eagleman, D. (2007). The effect of predictability on subjective duration. *PLoS ONE*, 2(11), 2–7. doi: 10.1371/journal.pone.0001264
- Paton, J. J., & Buonomano, D. V. (2018). The Neural Basis of Timing: Distributed Mechanisms for Diverse Functions. *Neuron*, 98(4), 687–705. doi: 10.1016/j.neuron.2018.03.045
- Pelli, D. G. (1997). *The VideoToolbox software for visual psychophysics: Transforming numbers into movies* (Vol. 10) (No. 4). doi: 10.1163/156856897X00366
- Penney, T. B., & Cheng, X. (2017). Duration Bisection: A User's Guide. In A. Vatakis, F. Balci, M. Di Luca, & A. Correa (Eds.), *Timing and time perception: Procedures, measures, and applicationt*. Brill.
- Poffenberger, A. T. (1912). *Reaction time to retinal stimulation: with special reference to the time lost in conduction through nerve centers*. Science Press.
- Poggel, D. A., Treutwein, B., Calmanti, C., & Strasburger, H. (2006). Increasing the temporal gain: Double-pulse resolution is affected by the size of the attention focus. *Vision Research*, 46(18), 2998–3008. doi: 10.1016/j.visres.2006.03.018
- Pöppel, E. (1997). A hierarchical model of temporal perception. *Trends in Cognitive Sciences*, 1(2), 56–61. doi: 10.1016/S1364-6613(97)01008-5
- Porter, T. C. (1902). Contributions to the study of flicker. paper ii. *Proceedings of the Royal Society of London*, 70(459-466), 313–329.
- Powers, A. R., Hillock, A. R., & Wallace, M. T. (2009). Perceptual Training Narrows the Temporal Window of Multisensory Binding. *Journal of Neuroscience*, 29(39), 12265–12274. doi: 10.1523/JNEUROSCI.3501-09.2009
- Poynter, D. (1989). Judging the Duration of Time Intervals: A Process of Remembering Segments of Experience. *Advances in Psychology*, 59(C), 305–331. doi: 10.1016/S0166-4115(08)61045-6
- Protopapa, F., Hayashi, M. J., Kulashekhar, S., & Zwaag, W. V. D. (2018). Chronotopic Maps in Human Medial Premotor Cortex. *bioRxiv*. doi: 10.1101/399857
- Pylyshyn, Z. W., & Storm, R. W. (1988). Tracking multiple independent targets: Evidence for a parallel tracking mechanism. *Spatial Vision*, 3(3), 179–197.
- Rahnev, D. A., Maniscalco, B., Luber, B., Lau, H., & Lisanby, S. H. (2012). Direct injection of noise to the visual cortex decreases accuracy but increases decision confidence. *Journal of Neurophysiology*, 107(6), 1556–1563. doi:

- 10.1152/jn.00985.2011
- Raij, T., Ahveninen, J., Lin, F.-H., Witzel, T., Jääskeläinen, I. P., Letham, B., . . . others (2010). Onset timing of cross-sensory activations and multisensory interactions in auditory and visual sensory cortices. *European Journal of Neuroscience*, *31*(10), 1772–1782.
- Rammsayer, T. H. (1994). Effects of practice and signal energy on duration discrimination of brief auditory intervals. *Perception & Psychophysics*, *55*(4), 454–464. doi: 10.3758/BF03205302
- Rammsayer, T. H., & Vogel, W. H. (1992). Pharmacologic Properties of the Internal Clock Underlying Time Perception in Humans. *Biological Psychology/Pharmacopsychology*, *26*, 71–80.
- Raviv, O., Ahissar, M., & Loewenstein, Y. (2012). How Recent History Affects Perception: The Normative Approach and Its Heuristic Approximation. *PLoS Computational Biology*, *8*(10). doi: 10.1371/journal.pcbi.1002731
- Raviv, O., Lieder, I., Loewenstein, Y., & Ahissar, M. (2014). Contradictory Behavioral Biases Result from the Influence of Past Stimuli on Perception. *PLoS Computational Biology*, *10*(12), 8–12. doi: 10.1371/journal.pcbi.1003948
- Recanzone, G. H., Makhama, S. D. D. R., & Guard, D. C. (1998). Comparison of relative and absolute sound localization ability in humans. *The Journal of the Acoustical Society of America*, *103*(2), 1085–1097. doi: 10.1121/1.421222
- Remijn, G., Van Der Meulen, G., Ten Hoopen, G., Nakajima, Y., Komori, Y., & Sasaki, T. (1999). On the robustness of time-shrinking. *Journal of the Acoustical Society of Japan (E)*, *20*(5), 365–373.
- Riggs, L. A., Volkman, F. C., & Moore, R. K. (1981). Suppression of the blackout due to blinks. *Vision Research*, *21*(7), 1075–1079. doi: 10.1016/0042-6989(81)90012-2
- Roach, N. W., Heron, J., & McGraw, P. V. (2006). Resolving multisensory conflict: A strategy for balancing the costs and benefits of audio-visual integration. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1598), 2159–2168. doi: 10.1098/rspb.2006.3578
- Roach, N. W., Heron, J., Whitaker, D., & McGraw, P. V. (2011). Asynchrony adaptation reveals neural population code for audio-visual timing. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1710), 1314–1322. doi: 10.1098/rspb.2010.1737
- Roach, N. W., McGraw, P. V., Whitaker, D. J., & Heron, J. (2017). Generalization of prior information for rapid Bayesian time estimation. *Proceedings of the National Academy of Sciences*, *114*(2), 412–417. doi: 10.1073/pnas.1610706114

- Ronconi, L., Oosterhof, N. N., Bonmassar, C., & Melcher, D. (2017). Multiple oscillatory rhythms determine the temporal organization of perception. *Proceedings of the National Academy of Sciences*, 201714522. doi: 10.1073/pnas.1714522114
- Rose, D., & Summers, J. (1995). Duration illusions in a train of visual stimuli. *Perception*, 24(10), 1177–1187. doi: 10.1068/p241177
- Roseboom, W., & Arnold, D. H. (2011). Twice Upon a Time: Multiple Concurrent Temporal Recalibrations of Audiovisual Speech. *Psychological Science*, 22(7), 872–877. doi: 10.1177/0956797611413293
- Roseboom, W., Kawabe, T., & Nishida, S. (2013). The cross-modal double flash illusion depends on featural similarity between cross-modal inducers. *Scientific Reports*, 3, 1–5. doi: 10.1038/srep03437
- Roseboom, W., Linares, D., & Nishida, S. (2015). Sensory adaptation for timing perception. *Proceedings of the Royal Society B: Biological Sciences*, 282(1805). doi: 10.1098/rspb.2014.2833
- Roufs, J. (1963). Perception lag as a function of stimulus luminance. *Vision Research*, 3(1-2), 81–91. doi: 10.1016/0042-6989(63)90070-1
- Ruskin, D. N., Bergstrom, D. a., Kaneoke, Y., Patel, B. N., Twery, M. J., & Walters, J. R. (1999). Multisecond oscillations in firing rate in the basal ganglia: robust modulation by dopamine receptor activation and anesthesia. *Journal of Neurophysiology*, 81(5), 2046–2055. doi: 0022-3077
- Rutschmann, J., & Link, R. (1964). Perception of temporal order of stimuli differing in sense mode and simple reaction time. *Perceptual and Motor Skills*, 18(2), 345–352.
- Rutschmann, R. (1966). Perception of temporal order and relative visual latency. *Science*, 152(3725), 1099–1101. doi: 10.1126/science.152.3725.1099
- Samaha, J., & Postle, B. R. (2015). The Speed of Alpha-Band Oscillations Predicts the Temporal Resolution of Visual Perception. *Current Biology*, 25(22), 2985–2990. doi: 10.1016/j.cub.2015.10.007
- Sasaki, T., Nakajima, Y., & Hoopen, G. T. E. N. (1998). Categorical Rhythm Perception as a Result of Unilateral Assimilation in Time-Shrinking. *Music Perception*, 16(2), 201–222.
- Sato, Y., Toyoizumi, T., & Aihara, K. (2007). Bayesian inference explains perception of unity and ventriloquism aftereffect: Identification of common sources of audiovisual stimuli. *Neural Computation*, 19(12), 3335–3355. doi: 10.1162/neco.2007.19.12.3335
- Sawai, K. I., Sato, Y., & Aihara, K. (2012). Auditory time-interval perception as causal inference on sound sources. *Frontiers in Psychology*, 3(NOV), 1–8. doi: 10.3389/fpsyg.2012.00524

- Scholl, B. J., Pylyshyn, Z. W., & Feldman, J. (2001). What is a visual object? Evidence from target merging in multiple object tracking. *Cognition*, *80*(1-2), 159–177. doi: 10.1016/S0010-0277(00)00157-8
- Schoups, A., Vogels, R., Qian, N., & Orban, G. (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature*, *412*(6846), 549–553. doi: 10.1038/35087601
- Schroeder, C. E., & Lakatos, P. (2009). Low-frequency neuronal oscillations as instruments of sensory selection. *Trends in Neurosciences*, *32*(1), 9–18. doi: 10.1016/j.tins.2008.09.012.Low-frequency
- Shankar, K. H., & Howard, M. W. (2010). Timing using temporal context. *Brain Res*, *1365*, 3–17. doi: 10.1016/j.brainres.2010.07.045
- Shioiri, S., & Cavanagh, P. (1990). ISI produces reverse apparent motion. *Vision Research*, *30*(5), 757–768. doi: 10.1016/0042-6989(90)90101-P
- Slutsky, D. A., & Recanzone, G. H. (2001). Temporal and spatial dependency, of the ventriloquism effect. *NeuroReport*, *12*(1), 7–10. doi: 10.1097/00001756-200101220-00009
- Smeets, J. B., Brenner, E., de Grave, D. D., & Cuijpers, R. H. (2002). Illusions in action: consequences of inconsistent processing of spatial attributes. *Experimental Brain Research*, *147*(2), 135–144.
- Soechting, J. F., & Lacquaniti, F. (1981). Invariant characteristics of a pointing movement in man. *Journal of Neuroscience*, *1*(7), 710–20. doi: 10.3389/fpsyg.2016.00020
- Sokolov, A., & Pavlova, M. (2003). Timing accuracy in motion extrapolation: Reverse effects of target size and visible extent of motion at low and high speeds. *Perception*, *32*(6), 699–706. doi: 10.1068/p3397
- Solomon, S. G., Martin, P. R., White, A. J. R., Rüttiger, L., & Lee, B. B. (2002). Modulation sensitivity of ganglion cells in peripheral retina of macaque. *Vision Research*, *42*(27), 2893–2898. doi: 10.1016/S0042-6989(02)00414-5
- Solomons, L. M. (1900). A new explanation of weber's law. *Psychological Review*, *7*(3), 234.
- Spence, C. (2013). Just how important is spatial coincidence to multisensory integration? Evaluating the spatial rule. *Annals of the New York Academy of Sciences*, *1296*(1), 31–49. doi: 10.1111/nyas.12121
- Spence, C., & Driver, J. (2004). *Crossmodal space and crossmodal attention*. Oxford University Press.
- Spence, C., & Parise, C. (2010). Prior-entry: A review. *Consciousness and cognition*, *19*(1), 364–379.

- Spencer, R. M., Karmarkar, U., & Ivry, R. B. (2009a). Evaluating dedicated and intrinsic models of temporal encoding by varying context. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1525), 1853–1863. doi: 10.1098/rstb.2009.0024
- Spencer, R. M., Karmarkar, U., & Ivry, R. B. (2009b). Evaluating dedicated and intrinsic models of temporal encoding by varying context. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1525), 1853–1863. doi: 10.1098/rstb.2009.0024
- Staddon, J. (2005). Interval timing: Memory, not a clock. *Trends in Cognitive Sciences*, 9(7), 312–314. doi: 10.1016/j.tics.2005.05.013
- Staddon, J., & Higa, J. (1999). Time and memory: towards a pacemaker-free theory of interval timing. *Journal of the Experimental Analysis of Behavior*, 71(2), 215–251. doi: 10.1901/jeab.1999.71-215
- Stephen, J. M., Aine, C. J., Christner, R. F., Ranken, D., Huang, M., & Best, E. (2002). Central versus peripheral visual field stimulation results in timing differences in dorsal stream sources as measured with MEG. *Vision Research*, 42(28), 3059–3074. doi: 10.1016/S0042-6989(02)00415-7
- Sternberg, S., Knoll, R. L., et al. (1973). The perception of temporal order: Fundamental issues and a general model. *Attention and performance IV*, 629–685.
- Stevenson, R. A., Zemtsov, R. K., & Wallace, M. T. (2012). Individual differences in the multisensory temporal binding window predict susceptibility to audiovisual illusions. *Journal of Experimental Psychology: Human Perception and Performance*, 38(6), 1517.
- Stone, J. V., Hunkin, N. M., Porrill, J., Wood, R., Keeler, V., Beanland, M., ... Porter, N. R. (2001). When is now? Perception of simultaneity. *Proceedings of the Royal Society B: Biological Sciences*, 268(1462), 31–38. doi: 10.1098/rspb.2000.1326
- Suetomi, D., & Nakajima, Y. (1998). *How stable is time-shrinking?* (Vol. 4) (No. 1).
- Suzuki, S., & Cavanagh, P. (1997). Focused attention distorts visual space: an attentional repulsion effect. *Journal of Experimental Psychology: Human Perception and Performance*, 23(2), 443.
- Taatgen, N. A., Van Rijn, H., & Anderson, J. (2007). An integrated theory of prospective time interval estimation: The role of cognition, attention, and learning. *Psychological Review*, 114(3), 577.
- Takeuchi, T., & De Valois, K. K. (1997). Motion-reversal reveals two motion mechanisms functioning in scotopic vision. *Vision Research*, 37(6), 745–755. doi: 10.1016/S0042-6989(96)00207-6
- Takeuchi, T., & De Valois, K. K. (2009). Visual motion mechanisms under low

- retinal illuminance revealed by motion reversal. *Vision Research*, 49(8), 801–809. doi: 10.1016/j.visres.2009.02.011
- Tappe, T., Niepel, M., & Neumann, O. (1994). A dissociation between reaction time to sinusoidal gratings and temporal-order judgment. *Perception*, 23(3), 335–347. doi: 10.1068/p230335
- Terao, M., Watanabe, J., Yagi, A., & Nishida, S. (2008). Reduction of stimulus visibility compresses apparent time intervals. *Nature Neuroscience*, 11(5), 541.
- Thorne, J. D., De Vos, M., Viola, F. C., & Debener, S. (2011). Cross-Modal Phase Reset Predicts Auditory Task Performance in Humans. *Journal of Neuroscience*, 31(10), 3853–3861. doi: 10.1523/JNEUROSCI.6176-10.2011
- Tiest, W. M. B., & Kappers, A. M. L. (2009). Tactile perception of thermal diffusivity. *Attention, perception & psychophysics*, 71(3), 481–489. doi: 10.3758/APP
- Treisman, M. (1963). Temporal Discrimination and the Indifference Interval: Implications for a Model of the "Internal Clock". *Psychological Monographs: General and Applied*, 77(31), 1.
- Treisman, M. (2013). The information-processing model of timing (treisman, 1963): Its sources and further development. *Timing & Time Perception*, 1(2), 131–158.
- Treisman, M., Faulkner, A., & Naish, P. L. (1992). On the relation between time perception and the timing of motor action: Evidence for a temporal oscillator controlling the timing of movement. *The Quarterly Journal of Experimental Psychology Section A*, 45(2), 235–263.
- Treisman, M., Faulkner, A., Naish, P. L., & Brogan, D. (1990). The internal clock: evidence for a temporal oscillator underlying time perception with some estimates of its characteristic frequency. *Perception*, 19(6), 705–743. doi: 10.1068/p190705
- Trommershäuser, J., Maloney, L. T., & Landy, M. S. (2003). Statistical decision theory and the selection of rapid, goal-directed movements. *Journal of the Optical Society of America A*, 20(7), 1419. doi: 10.1364/JOSAA.20.001419
- Tsao, A., Sugar, J., Lu, L., Wang, C., Knierim, J. J., Moser, M.-B., & Moser, E. I. (2018). Integrating time from experience in the lateral entorhinal cortex. *Nature*. doi: 10.1038/s41586-018-0459-6
- Tse, P. U., Intriligator, J., Rivest, J., & Cavanagh, P. (2004). Attention and the subjective expansion of time. *Perception and Psychophysics*, 66(7), 1171–1189. doi: 10.3758/BF03196844
- Tyler, C. W. (1985). Analysis of visual modulation sensitivity. II. Peripheral retina and the role of photoreceptor dimensions. *Journal of the Optical Society of America A*, 2(3), 393–398. doi: 10.1364/JOSAA.2.000393
- Üstün, S., Kale, E. H., & Çiçek, M. (2017). Neural Networks for Time Perception



- and Working Memory. *Frontiers in Human Neuroscience*, 11(February), 1–11. doi: 10.3389/fnhum.2017.00083
- Van De Grind, W. (2002). Physical, neural, and mental timing. *Consciousness and Cognition*, 11(2), 241–264. doi: 10.1006/ccog.2002.0560
- van der Burg, E., Alais, D., & Cass, J. (2015). Audiovisual temporal recalibration occurs independently at two different time scales. *Scientific Reports*, 5, 1–7. doi: 10.1038/srep14526
- van der Burg, E., Orchard-Mills, E., & Alais, D. (2014). Rapid temporal recalibration is unique to audiovisual stimuli. *Experimental Brain Research*, 233(1), 53–59. doi: 10.1007/s00221-014-4085-8
- Van Eijk, R. L., Kohlrausch, A., Juola, J. F., & Van De Par, S. (2008). Audiovisual synchrony and temporal order judgments: Effects of experimental method and stimulus type. *Perception and Psychophysics*, 70(6), 955–968. doi: 10.3758/PP.70.6.955
- Van Wassenhove, V. (2009). Minding Time in an amodal representational space. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1525), 1815–1830. doi: 10.1098/rstb.2009.0023
- Van Wassenhove, V., & Lecoutre, L. (2015). Duration estimation entails predicting when. *NeuroImage*, 106, 272–283. doi: 10.1016/j.neuroimage.2014.11.005
- van der Burg, E., Alais, D., & Cass, J. (2013). Rapid recalibration to audiovisual asynchrony. *Journal of neuroscience*, 33(37), 14633–14637.
- van der Burg, E., Alais, D., & Cass, J. (2018). Rapid recalibration to audiovisual asynchrony follows the physical—not the perceived—temporal order. *Attention, Perception, and Psychophysics*(September), 1–9. doi: 10.3758/s13414-018-1540-9
- van Rijn, H., & Taatgen, N. A. (2008). Timing of multiple overlapping intervals: How many clocks do we have? *Acta Psychologica*, 129(3), 365–375. doi: 10.1016/j.actpsy.2008.09.002
- VanRullen, R. (2016). Perceptual Cycles. *Trends in Cognitive Sciences*, 20(10), 723–735. doi: 10.1016/j.tics.2016.07.006
- van Wassenhove, V. (2016). Temporal cognition and neural oscillations. *Current Opinion in Behavioral Sciences*, 8(February), 124–130. doi: 10.1016/j.cobeha.2016.02.012
- van Wassenhove, V., Buonomano, D. V., Shimojo, S., & Shams, L. (2008). Distortions of subjective time perception within and across senses. *PLoS ONE*, 3(1). doi: 10.1371/journal.pone.0001437

- van Wassenhove, V., Grant, K. W., & Poeppel, D. (2007). Temporal window of integration in auditory-visual speech perception. *Neuropsychologia*, *45*(3), 598–607. doi: 10.1016/j.neuropsychologia.2006.01.001
- Varela, F. J., Toro, A., Roy John, E., & Schwartz, E. L. (1981). Perceptual framing and cortical alpha rhythm. *Neuropsychologia*, *19*(5), 675–686. doi: 10.1016/0028-3932(81)90005-1
- Vatakis, A., Navarra, J., Soto-Faraco, S., & Spence, C. (2007). Temporal recalibration during asynchronous audiovisual speech perception. *Experimental Brain Research*, *181*(1), 173–181. doi: 10.1007/s00221-007-0918-z
- Victor, J. D., & Conte, M. M. (2002). Temporal phase discrimination depends critically on separation. *Vision Research*, *42*(17), 2063–2071. doi: 10.1016/S0042-6989(02)00125-6
- Vidal, M. (2017). Hearing Flashes and seeing beeps: Timing audiovisual events. *PLoS ONE*, *12*(2), 1–19. doi: 10.1371/journal.pone.0172028
- Viviani, P., & Aymoz, C. (2001). Colour, form, and movement are not perceived simultaneously. *Vision Research*, *41*(22), 2909–2918. doi: 10.1016/S0042-6989(01)00160-2
- Viviani, P., & Flash, T. (1995). Minimum-jerk, two-thirds power law, and isochrony: converging approaches to movement planning. *Journal of Experimental Psychology: Human Perception and Performance*, *21*(1), 32.
- Vroomen, J., & Keetels, M. (2010). Perception of intersensory synchrony: a tutorial review. *Attention, Perception, & Psychophysics*, *72*(4), 871–884.
- Vroomen, J., Keetels, M., De Gelder, B., & Bertelson, P. (2004). Recalibration of temporal order perception by exposure to audio-visual asynchrony. *Cognitive Brain Research*, *22*(1), 32–35. doi: 10.1016/j.cogbrainres.2004.07.003
- Walker, J. T., Irion, A. L., & Gordon, D. G. (1981). Simple and contingent aftereffects of perceived duration in vision and audition. *Perception & Psychophysics*, *29*(5), 475–486. doi: 10.3758/BF03207361
- Wang, C., Xiao, Y., Burdet, E., Gordon, J., & Schweighofer, N. (2016). The duration of reaching movement is longer than predicted by minimum variance. *Journal of Neurophysiology*, *116*(5), 2342–2345. doi: 10.1152/jn.00148.2016
- Watson, A. B. (1986). Temporal sensitivity. In K. Boff, L. Kaufman, & J. P. Thomas (Eds.), *Handbook of perception and human performance* (pp. 6–1). Wiley, New York.
- Watson, A. B., & Nachmias, J. (1977). Patterns of temporal interaction in the detection of gratings. *Vision Research*, *17*(8), 893–902. doi: 10.1016/0042-6989(77)90063-3
- Wearden, J. (2016). *The psychology of time perception*. Springer.

- Wearden, J., & Penton-Voak, I. (1995). Feeling the Heat: Body Temperature and the Rate of Subjective Time, Revisited. *The Quarterly Journal of Experimental Psychology Section B*, 48(2), 129–141. doi: 10.1080/14640749508401443
- Welch, R. B., & Warren, D. H. (1980). Immediate perceptual response to intersensory discrepancy. *Psychological Bulletin*, 88(3), 638–667. doi: 10.1037/0033-2909.88.3.638
- Wenke, D., & Haggard, P. (2009). How voluntary actions modulate time perception. *Experimental Brain Research*, 196(3), 311–318. doi: 10.1007/s00221-009-1848-8
- Westheimer, G. (1975). Visual Acuity and Hyperacuity. *Investigative Ophthalmology*, 64(8), 570–572. doi: 10.1097/00006324-198708000-00002
- Westheimer, G. (1983). Temporal order detection for foveal and peripheral visual stimuli. *Vision Research*, 23(8), 759–763. doi: 10.1016/0042-6989(83)90197-9
- Westheimer, G. (1999). Discrimination of short time intervals by the human observer. *Experimental Brain Research*, 129(1), 121–126. doi: 10.1007/s002210050942
- Westheimer, G., & Levi, D. M. (1987). Depth attraction and repulsion of disparate foveal stimuli. *Vision Research*, 27(8), 1361–1368. doi: 10.1016/0042-6989(87)90212-4
- Williams, J. M., & Lit, A. (1983). Luminance-dependent visual latency for the hess effect, the pulfrich effect, and simple reaction time. *Vision Research*, 23(2), 171–179. doi: 10.1016/0042-6989(83)90140-2
- Wolpert, D. M. (1997). Computational approaches to motor control. *Trends in Cognitive Science*, 1(6), 209–216. doi: 10.1016/S1364-6613(97)01070-X
- Wozny, D. R., Beierholm, U. R., & Shams, L. (2010). Probability matching as a computational strategy used in perception. *PLoS Computational Biology*, 6(8). doi: 10.1371/journal.pcbi.1000871
- Wright, B. A., Lombardino, L. J., King, W. M., Puranik, C. S., Leonard, C. M., & Merzenich, M. M. (1997). Deficits in auditory temporal and spectral resolution in language impaired children. *Nature*, 387, 176–178. doi: 10.1038/387176a0
- Wright, B. A., & Sabin, A. T. (2007). Perceptual learning: how much daily training is enough? *Experimental Brain Research*, 180(4), 727–736.
- Wu, S.-W., Dal Martello, M. F., & Maloney, L. T. (2009). Sub-optimal allocation of time in sequential movements. *PloS one*, 4(12), e8228.
- Wu, S.-W., Trommershäuser, J., Maloney, L. T., & Landy, M. S. (2006). Limits to human movement planning in tasks with asymmetric gain landscapes. *Journal of Vision*, 6(1), 5. doi: 10.1167/6.1.5

- Xiao, L. Q., Zhang, J. Y., Wang, R., Klein, S. A., Levi, D. M., & Yu, C. (2008). Complete Transfer of Perceptual Learning across Retinal Locations Enabled by Double Training. *Current Biology*, *18*(24), 1922–1926. doi: 10.1016/j.cub.2008.10.030
- Yakimoff, N., Mateeff, S., Ehrenstein, W. H., & Hohnsbein, J. (1993). Motion Extrapolation Performance: A Linear Model Approach. *Human Factors*, *35*(3), 501–510. doi: 10.1177/001872088502700306
- Yarrow, K., Haggard, P., Heal, R., Brown, P., & Rothwell, J. C. (2001). Illusory perceptions of space and time preserve cross-saccadic perceptual continuity. *Nature*, *414*(6861), 302–305. doi: 10.1038/35104551
- Yarrow, K., Jahn, N., Durant, S., & Arnold, D. H. (2011). Shifts of criteria or neural timing? The assumptions underlying timing perception studies. *Consciousness and Cognition*, *20*(4), 1518–1531. doi: 10.1016/j.concog.2011.07.003
- Yarrow, K., Martin, S. E., Di Costa, S., Solomon, J. A., & Arnold, D. H. (2016). A roving dual-presentation simultaneity-judgment task to estimate the point of subjective simultaneity. *Frontiers in Psychology*, *7*(MAR), 1–19. doi: 10.3389/fpsyg.2016.00416
- Yarrow, K., Minaei, S., & Arnold, D. H. (2015). A model-based comparison of three theories of audiovisual temporal recalibration. *Cognitive Psychology*, *83*, 54–76. doi: 10.1016/j.cogpsych.2015.10.002
- Yarrow, K., & Rothwell, J. (2003). Manual Chronostasis: Tactile Perception Precedes Physical Contact. *Current Biology*, *13*, 1134–1139. doi: 10.1016/S
- Yarrow, K., Whiteley, L., Haggard, P., & Rothwell, J. C. (2006). Biases in the perceived timing of perisaccadic perceptual and motor events. *Perception and Psychophysics*, *68*(7), 1217–1226. doi: 10.3758/BF03193722
- Yeshurun, Y., & Levy, L. (2003). TRANSIENT SPATIAL ATTENTION DEGRADES TEMPORAL RESOLUTION Yaffa Yeshurun and Liat Levy. *Psychological Science*, 225–231.
- Yeung, N., & Summerfield, C. (2012). Metacognition in human decision-making: Confidence and error monitoring. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1594), 1310–1321. doi: 10.1098/rstb.2011.0416
- Yuan, X., Li, B., Bi, C., Yin, H., & Huang, X. (2012). Audiovisual temporal recalibration: Space-based versus context-based. *Perception*, *41*(10), 1218–1233. doi: 10.1068/p7243
- Zakay, D., & Block, R. A. (2004). Prospective and retrospective duration judgments: An executive-control perspective. *Acta Neurobiologiae Experimentalis*, *64*(3), 319–328.

- Zampini, M., Guest, S., Shore, D. I., & Spence, C. (2005). Audio-visual simultaneity judgments. *Perception and Psychophysics*, *67*(3), 531–544. doi: 10.3758/BF03193329
- Zampini, M., Shore, D. I., & Spence, C. (2003). Audiovisual temporal order judgments. *Experimental Brain Research*, *152*(2), 198–210. doi: 10.1007/s00221-003-1536-z
- Zhang, H., Wu, S.-W., & Maloney, L. T. (2010). Planning multiple movements within a fixed time limit: The cost of constrained time allocation in a visuo-motor task. *Journal of Vision*, *10*(6), 1–1.

## Résumé

Les événements pertinents de notre environnement sont intégrés au flux d'information complexe et multisensoriel qui nous parvient. La perception du temps est malléable et de nombreuses illusions suggèrent que le temps perçu est influencé par le contexte. Dans le cadre de cette thèse, nous nous sommes intéressés à l'influence de différents aspects du contexte sur la perception du temps et du timing des actions chez l'humain. Dans la première partie de cette thèse, nous avons étudié le rôle du caractère explicite de l'apparition d'un événement sur la durée perçue de l'intervalle entre deux événements. Nous avons montré que l'influence du contexte temporel était plus forte dans la condition d'apparition implicite, pour laquelle le biais d'estimation des vers la moyenne des durées présentées est plus fort, et la sensibilité plus basse. Dans la deuxième partie de la thèse, nous avons étudié les effets du contexte temporel et spatial sur le temps perçu des événements. Les résultats de ces études suggèrent que le moment perçu de l'apparition d'un événement ne correspond pas toujours aux latences perceptives mesurées par des tâches de temps de réaction, et que la saillance est un indice important pour percevoir le temps. Enfin, dans la troisième partie, nous avons examiné comment différentes sources d'incertitude influencent le timing perçu d'une action et son auto-évaluation. Les résultats suggèrent que ces deux aspects s'appuieraient au moins en partie sur des processus différents.

## Mots Clés

perception du temps, perception, vision, action, audition

## Abstract

Relevant events in our environment are embedded in the complex, multi-sensory stream of information. Time perception is malleable, and numerous time illusions suggest that the perceived time of events is affected by context. The work presented in this thesis investigated how different aspects of human time perception and timing an action are affected by context. In the first part of the thesis, we investigated how the explicitness of the event onset affects perceived elapsed time between two points in time. The temporal context affected the estimates more in the implicit onset condition. The estimates were more biased towards the mean of the presented durations, and sensitivity of duration discrimination sensitivity was lower in the condition with no explicit onset of the duration to be timed. The effects of the temporal and spatial context on the perceived time of events were addressed in the second part. The findings suggest that the perceived time of events can be easily and compulsory biased by the temporal and spatial context. Findings from these studies support the hypothesis that the perceived time of events does not always correspond to the perceptual latencies measured in the reaction time tasks, and that the saliency is an important cue for the perceived time. Finally, in the third part, we investigated how different sources of uncertainty affect the timing and self-evaluation of an action. The findings suggest that timing an action and evaluating its outcome may, at least in part, rely on different computations.

## Keywords

time perception, perception, vision, action, audition