It’s About Time

Studying the Encoding of Duration

Jim Maarseveen

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Studying the Encoding of Duration

Over tijd:
Een studie naar de codering van tijdsduur

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Colofon

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Studying the Encoding of Duration

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“Time has passed, and something happened”

– Stewart Graham Lee, 2014 –

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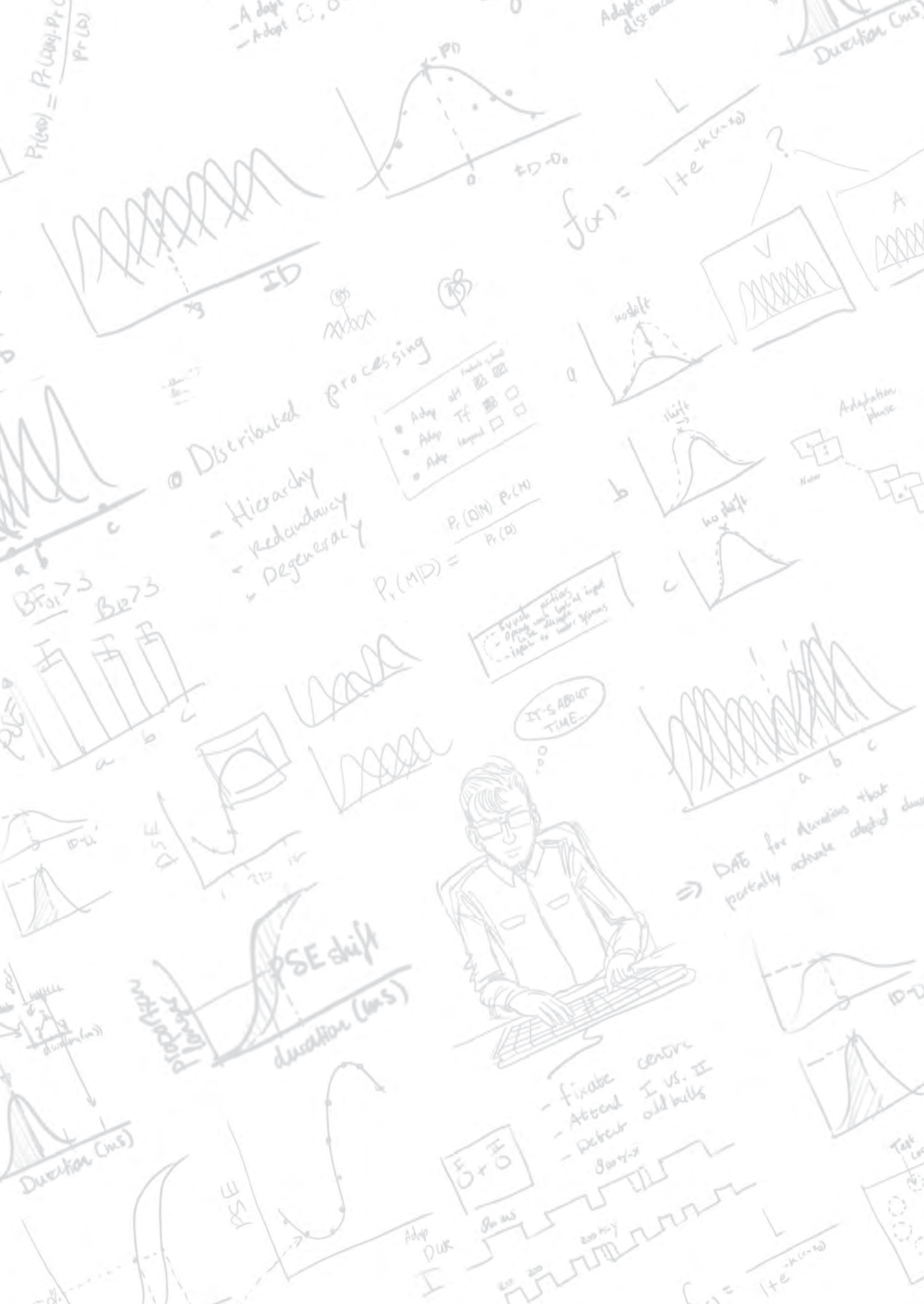

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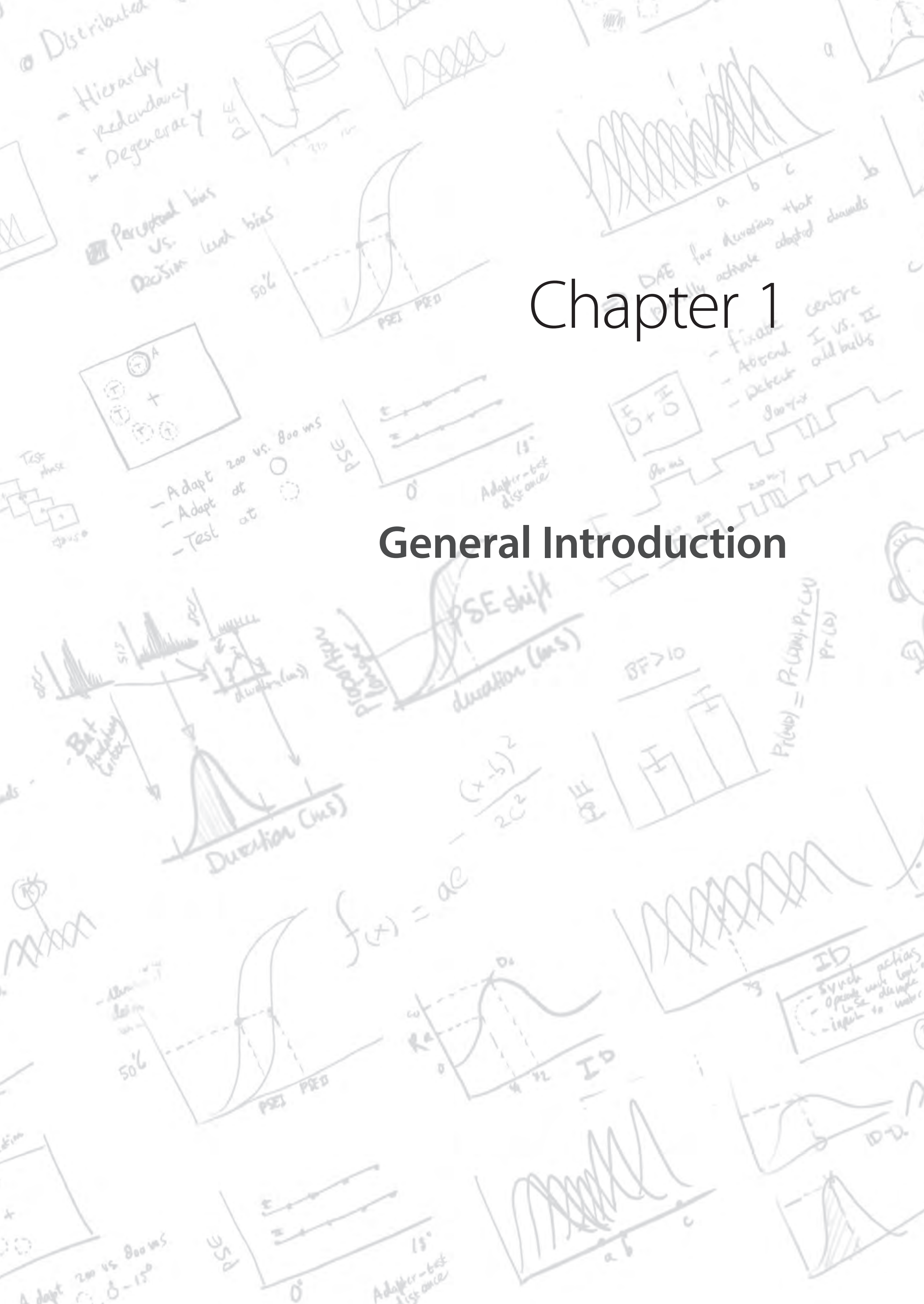


Chapter 1

General Introduction

Time is of the essence

The passage of time is a fundamental aspect of the human experience. We all experience ourselves as moving through time, going from one moment to the next, making our way into the future. As part of this process we experience time at many different scales. We live for many years and spend a lot of our time planning the coming months, weeks, days, hours, and minutes of our lives. At the same time, we have learned to understand the passage of time at timescales that are beyond the limits of our experience. For example, we have estimated that our sun will die and turn into a black hole in approximately 10 billion years. On the opposite end of this spectrum, we understand (sub) molecular processes that occur at an infinitely small timescale such as nuclear fission lasting only 10^{-14} seconds. However, it is our perception of time at the most immediate timescale available to us, the passing of (milli)seconds, that governs our existence. Our experience of time at the (sub-)second timescale is crucial for our interaction with the world around us. It allows us to analyze whether events occur at the same time (simultaneity) or at separate moments; to judge the temporal order of events; and to perceive temporal properties such as the duration of events and the rate at which things change over time. We can then use this temporal information to learn about the temporal regularities in our environment and apply this knowledge to predict future events, plan our actions, and guide our decisions. Furthermore, our perception of temporal information allows us to track our behavior and synchronize our actions with our environment. Consider a simple action such as catching a ball. When a ball is thrown at us, it moves closer over time. Since we perceive separated moments in time and can judge their temporal relation, we can infer that the ball is moving towards us. If necessary, we can then use our knowledge of temporal patterns to estimate the speed at which the ball is moving and the time we have left until the ball reaches us. This allows us to synchronize our movements with the external event and try and catch the ball. This example provides a fitting description of the multiple facets of our temporal perception that we use to successfully interact with the world around us.

The perception of duration

it is clear that perceiving temporal information entails processing several related but different types of information (i.e. simultaneity, order, duration). For example, it is possible to perceive that two things happened in a certain order, without knowing how much time has passed between the two events. As such, different types of temporal information are best considered separately in order to understand the individual components properly. In the current dissertation we focus primarily on the perception of duration. Understanding the duration of an event, as well as the duration between events is key to understanding the temporal structure of our environment. The time between our actions and events in the world, inform us whether they are likely to be causally related. Furthermore, our ability to act at the right time based on cues from the environment is crucial in producing successful interactions. Without duration perception, we would not be able to understand how our behavior relates to the outcomes that we create, making it impossible to learn from our actions.

To study duration perception, it is important to understand what duration is, and how it can be measured. Duration is often defined as the time during which something exists or lasts. In other words, it reflects the amount of time that has passed between two successive events (i.e. the beginning and end of a stimulus). However, this passage of time is not a physical property that can be measured directly. Instead, duration is derived from periodic or predictable changes in the physical world that are consistently measurable at different points in time. For example, the SI definition of a single second is 'the duration of 9 192 631 770 periods of the radiation corresponding to the transition between the two hyperfine levels of the ground state of the cesium 133 atom'. This property of duration is mirrored in our perception of duration. Since there is no physical carrier of duration information that can be detected, humans do not possess a sensory structure dedicated to perceiving duration. Instead, information about duration can only be derived from changes in sensory information that are encoded by existing sensory structures (e.g. the visual system). In other words, understanding duration perception entails understanding the way in which duration information is encoded from different sources of sensory information.

Models of duration encoding

researchers have proposed different models to describe how information about duration can be derived from sensory input. Often these models are modular, proposing dedicated mechanisms that extract the duration of an event (Ivry, 1996; Ivry & Schlerf, 2008; Matell & Meck, 2004; Miall, 1989). The oldest and more widespread models assume a dedicated clock-like timing system in the brain (Gibbon, 1977; Treisman, 1963). According to these models, the brain contains a pacemaker-like unit which generates pulses at a steady rate. When timing an event, these pulses are collected by a so-called accumulator from the moment the event starts until it ends. After this, the accumulated pulses provide a code for the duration of the event that can be stored and used to guide behavior. Other dedicated models have proposed mechanisms such as coincidence detection in banks of oscillators (Ivry, 1996; Matell & Meck, 2004; van Rijn, Gu, & Meck, 2014) or differential patterns of activity in a set of delay lines (Desmond & Moore, 1988).

Another line of theories is based on the idea that dedicated systems for duration encoding are not required (Buonomano & Laje, 2010; Karmarkar & Buonomano, 2007). Instead, these theories focus on the intrinsic temporal properties of the sensory signals being processed by the brain. According to the State Dependent Network (SDN) model, duration is encoded implicitly in the way that activity in a (neural) network changes over time. Even when presented with a stimulus that does not change, the response of the neural network responding to that stimulus will change over time. As such, these changes in neural responses provide an implicit signal for the passage of time while a stimulus is present. By learning the network states that are associated with specific stimulus durations, the duration of stimuli can be interpreted without a dedicated system that extracts information about time. In other words, the SDN model propose that temporal information is encoded in spatiotemporal patterns of activity without the need to explicitly encode or store information about duration. Yet, another type of intrinsic duration model relies on the endogenous neural oscillations naturally present in our brain (Herbst & Landau, 2016). Similar to the SDN model, the change in activity associated with neural oscillations provides an implicit signal for the passage of time that could be leveraged to track the duration of events.

The duration channel model of duration perception

Another promising model is the *duration channel model of duration perception*. According to the duration channel model the encoding and processing of duration information mirrors the encoding of other non-temporal features. More specifically, it postulates the existence of duration-tuned neurons that show optimal tuning to a range of sub-second durations (Heron et al., 2012; Ivry, 1996). When presented with an event these duration-tuned neurons respond selectively depending on their preferred duration (figure 1a). This means that a duration-tuned neuron with a preferred duration of 100 will respond vigorously to events lasting 100 ms, but will show increasingly less activity to events with durations that are shorter/longer than 100 ms. These duration-tuned neurons are grouped into 'duration channels', with each channel showing duration-tuning to a distinct duration (figure 1b). By reading out the relative activation of these duration channels the duration of events can be encoded (figure 2). The resulting population response provides an explicit representation of duration that can be used for further processing.

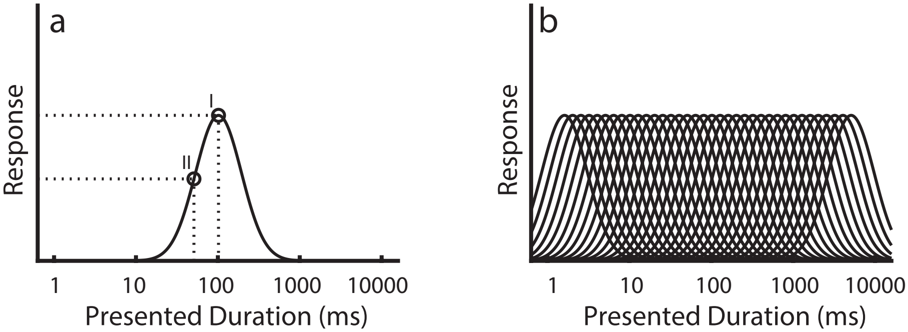


Figure 1. a) A single duration-tuned neuron's potential response as a function of the presented duration. The neuron responds strongest when presented with its preferred duration (I). When presented with shorter or longer duration, the response weakens (II). b) A bank of duration channels each with a different preferred duration represented by the peak of the distribution.

This mechanism that relies on duration-tuned neurons is very similar to the mechanisms that have been shown to underlie the encoding of a range of other sensory features such as orientation (Gibson, 1937; Hubel & Wiesel, 1959), motion direction (Albright, 1984; Anstis, Verstraten, & Mather, 1998), pitch (Romani, Williamson, & Kaufman, 1982), and numerosity (Burr & Ross, 2008; Harvey, Klein, Petridou, & Dumoulin, 2013). In other words, the duration channel model proposes a biologically plausible mechanism that is used to solve computational challenges throughout the brain. As is the case for any channel-based encoding model, the channel-based encoding of duration confers several advantages for efficient and robust encoding. Firstly, the usage of relative activation to encode duration is robust to absolute changes in the activity level of individual channels, such as those that might occur when events differ in overall salience or intensity. Secondly, using population responses allows the system to interpolate across individual channels resulting in a higher accuracy than that predicted by the individual channels. Thirdly, channel-based encoding requires overlap in the preferred duration of individual channels leading to a redundancy that makes the system more robust to noise in a single channel. This property also makes the system more resilient to damage, because duration can still be encoded effectively if only a subset of the channels is still functioning. The biological plausibility of channel-based encoding coupled with the above processing advantages provide a compelling motivation to explore the idea that duration-tuned mechanisms underlie the encoding of duration. In addition, the channel-based model of duration encoding provides clear predictions for timing behavior and neural responses to duration that can be empirically tested.

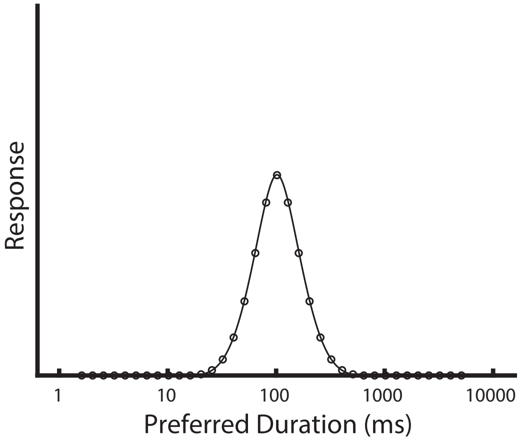


Figure 2. The population response of a bank of duration-tuned channels to a particular duration (100 ms) as a function of the channels' preferred duration. Each marker represents the response of a single channel, the fitted line is added for visualisation purposes. The relative activation across the duration-tuned channels provide a population response that signals the most likely perceived duration.

Sensory adaptation and the duration after-effect

A generally acknowledged method to study feature-tuned mechanisms in the human brain behaviorally is via the method of sensory adaptation. Sensory adaptation refers to prolonged or repeated presentation of a single value of a stimulus feature (e.g. a particular orientation or tone) with the goal of measuring the effect of this repeated stimulation on the observer's perception of that feature. From these measurements, it is possible to infer the properties of the underlying mechanisms responsible for the encoding of that feature. In the case of feature-tuned channels, sensory adaptation is predicted to lead to a so called *repulsive* after-effect. For example, in the tilt after-effect prolonged stimulation with the same orientation leads to a subsequently presented orientation to appear more distinct from the adapted orientation (Gibson, 1937). This after-effect is believed to result from sensory adaptation in a particular set of orientation channels. Presenting the system with the same orientation input causes groups of neurons tuned to that orientation to show a reduced response to the presented stimulus. Because this reduced response does not affect the weighted population response to the presented stimulus, it does not change the perception of that particular orientation. However, presenting orientations that are different but partially activate the same channels leads to a shift in the population response. This causes orientations that differ slightly from the adapted orientation to be perceived as more distinct. At the same time, the perception of orientations that do not activate the adapted population is unaffected. This method has been used to study sensory processing in different sensory modalities and has proven to be helpful in understanding the processing of a range of sensory features.

To summarize, sensory adaptation allows us to probe the underlying neural structure responsible for feature encoding by adapting the system to a specific value of a feature and measuring the behavioral consequences. This has led to after-effects being referred to as the psychologist's micro electrode (Frisby, 1979).

Similar to the after-effects described above, a channel-based model of duration encoding predicts a repulsive duration after-effect (DAE) following adaptation to duration. In this case, adaptation to a certain duration is predicted to cause a decreased response in a subset of duration-channels sensitive to that specific duration (figure 3a). Again, because this decreased response does not affect the population response to the adapted stimulus, it does not change the observer's perception of the adapted duration (figure 3b). However, durations that partially activate the adapted channels will be perceived as more distinct from the adapted duration (figure 3c). In other words, durations that are slightly shorter than the adapted duration should appear even shorter, while duration that are slightly longer should appear even longer. Furthermore, this effect should be limited to durations that partially activate the adapted channels, with no changes in the perception of much shorter or much longer durations (figure 3d).

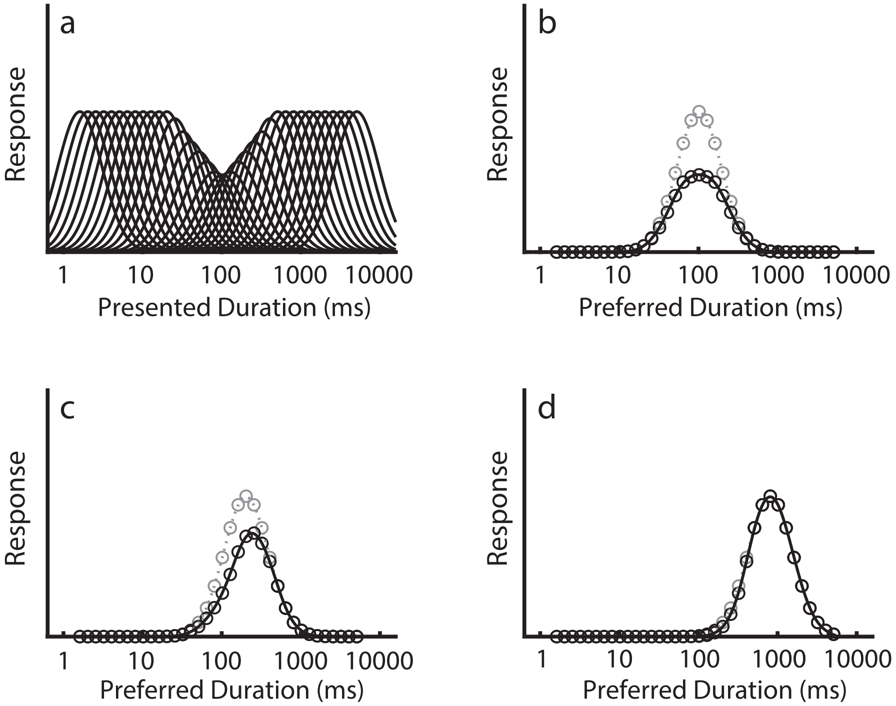


Figure 3. a) A bank of duration channels each with a different preferred duration represented by the peak of each distribution. The potential response of each channel has changed as the result of sensory adaptation, with the largest changes for channels whose preferred duration matched the adaptation duration (100 ms). Each of the other images (b,c,d) show the population response of a bank of duration-tuned channels to a particular duration as a function of the channels' preferred durations. Each marker represents the response of a single channel, the fitted line is added for visualisation purposes. The relative activation in each of the channels represents the population response of all the channels to that particular duration. The grey lines and associated markers display the population response for unadapted channels for comparison to an unadapted state. b) The population response for a presented duration equal to the adapted duration. The overall population response dampens, but the relative activation across different channels stays the same. As a result, the duration perceived by the observer remains unchanged. c) The population response for a presented duration that differs from the adapted duration. Since this duration partially activates the adapted channels, the population response shifts away from the adapted duration. As a result, the presented duration is perceived as more distinct from the adapted duration. d) The population response for a presented duration that differs from the adapted duration. Since this duration no longer partially activates the adapted channels, the population response does not change. As a result, the duration perceived by the observer remains unchanged.

In line with the prediction outlined above, several studies have demonstrated that adaptation to duration leads to a subsequent repulsive DAE (Heron et al., 2012; Heron, Hotchkiss, Aaen-Stockdale, Roach, & Whitaker, 2013; Li, Yuan, & Huang, 2015; Shima, Murai, Hashimoto, & Yotsumoto, 2016). These studies have repeatedly demonstrated that adaptation to a particular duration in one modality causes the perceived duration of subsequent durations in that same modality to shift away from the adapted duration. For example, after adapting to a visual event lasting 400 ms, the perceived duration of visual events with a shorter duration (i.e. 200 ms) will decrease, while the perceived duration of events with a longer duration (i.e. 800 ms) will increase. Heron et al. (2012) measured duration adaptation over a wider range of durations (40 – 2560 ms) and found that the DAE only occurred when the adapted duration was close to the tested duration, disappearing when the difference between adapter and test duration became too large (Figure 4). This result shows that duration channels have a limited tuning bandwidth, with adaptation affecting duration perception only when subsequent presentation fall within the bandwidth of the adapted channels. Together, these demonstrations of sensory adaptation for duration provide strong evidence for the existence of duration-tuned mechanisms that underlie the encoding of duration.

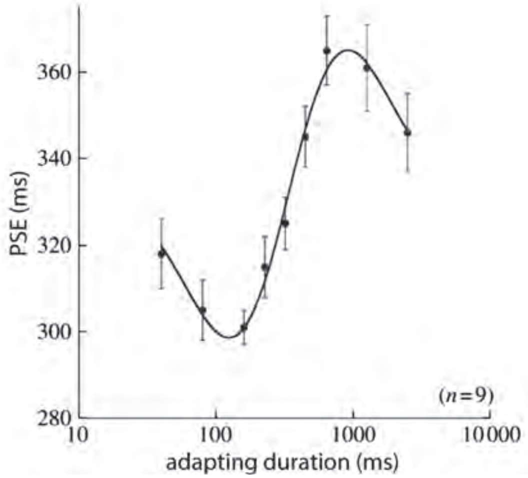


Figure 4. The DAE measured for adaptation to a range of durations (40 – 2560 ms). The Point of Subjective Equality (PSE) is plotted as a function of the adaptation durations. All DAE measurements are in reference to a 320ms auditory reference stimulus. PSEs lower than 320ms indicate an increase in perceived duration of the test stimulus, while PSEs higher than 320ms indicate a decrease in perceived duration of the test stimulus. Adapted from Heron, et al. (2012).

Additional evidence for duration-tuned responses

Additional behavioral evidence for channel-based encoding of duration comes from studies demonstrating duration-specific training benefits. Following duration discrimination training, participants show improved duration sensitivity and reduced performance variability on the trained durations, but not on untrained counterparts (Bueti & Buonomano, 2014; Karmarkar & Buonomano, 2003; Nagarajan, Blake, Wright, Byl, & Merzenich, 1998; Wright et al., 1997). Similar to the adaptation results, these selective training benefits could reflect changes in the duration-tuned mechanism that facilitate duration encoding for the trained durations (Bueti & Buonomano, 2014). Even more evidence is provided by neurophysiological studies in animals and fMRI in humans. For example, animal studies have demonstrated duration-tuned single neurons in cat auditory cortex (He, Hashikawa, Ojima, & Kinouchi, 1997), cat visual cortex (Duysens, Schaafsma, & Orban, 1996), and brown bat auditory cortex (Ehrlich, Casseday, & Covey, 1997; Wu & Jen, 2008). In addition, two studies in non-human primates have reported duration-tuned responses in cells in the medial pre-motor cortex during a rhythmic tapping task (Merchant, Pérez, Zarco, & Gámez, 2013) and in the (pre-)supplementary motor areas during an interval-generation task (Mita, Mushiake, Shima, Matsuzaka, & Tanji, 2009). More recently, these findings have been elaborated upon by human fMRI studies that demonstrate duration-selective responses in several cortical areas. Hayashi and colleagues, for example, used an fMRI adaptation paradigm to demonstrate a decreased BOLD-response in the (right) inferior parietal lobule (IPL) following repetitions of identical duration (Hayashi et al., 2015). This adaptation did not occur when the two durations were different, indicating that the BOLD-responses in this area reflected selective responses to specific durations. This finding was further corroborated by a recent study that used multivariate pattern analysis to demonstrate above chance classification of presented durations in the left and right IPL, the right superior parietal lobule (SPL), the right inferior frontal gyrus (IFG), and medial frontal cortex (MFC). Additionally, this study reported that individual decoding accuracy in the right parietal cortex correlated with participants' task performance on a duration judgment task (Hayashi, van der Zwaag, Bueti, & Kanai, 2018), further underscoring the role of parietal areas in the encoding of duration. Finally, a recent study by Protopapa et al., (2018) reported duration-tuned activity in supplementary motor area (SMA) and inferior parietal sulcus (IPS).

These duration-tuned responses were spatially organized demonstrating chronotropic organization in the brain. This type of topographic organization is often reported for stimulus features that are encoded by feature-tuned neural substrates, such as columnar organization in V1 (Yacoub, Harel, & Ugurbil, 2008) and topographical representations of numerosity (Harvey et al., 2013).

Using the DAE to probe duration encoding

The studies I have described so far, provide converging evidence for the notion that duration-tuned mechanisms play a role in the encoding of duration. However, so far our understanding of the exact nature of these duration-tuned mechanisms and how they operate is rather limited. For one, many of the assumptions of the duration channel model are based on existing knowledge about the processing of non-temporal sensory features such as orientation and spatial frequency. However, is unknown as to what extent duration-tuned neural structures will mirror the structural and functional properties of the neural structures involved in the encoding of these other sensory features. For example, many of the well-studied visual features such as orientation are encoded by low-level visual areas that show a high level of structural and functional organization. In contrast, feature-tuned encoding of numerosity seems to rely on a more distributed processing network located throughout the association cortex (Harvey & Dumoulin, 2016). Similarly, it is unclear what visual information (or neural input) is used by the brain to extract duration information. Further study is required to understand these basic properties of the duration channel model.

It is also unclear how the duration channel model and empirical findings such as the DAE relate to other findings reported in the duration perception literature. As described earlier, there is a wide range of models that has been used to predict and explain findings within the field of duration perception. In many cases, these models (and the related paradigms) rely on unique mechanisms that predict empirical findings that are not easily explained by the duration channel model. In addition, there is a large body of work on timing behavior and temporal illusions that cannot readily be explained by the duration channel model in its current form. This raises questions about the role of duration-tuned mechanisms in our overall ability to encode, store, and use duration information. Answering these questions properly requires a deeper understanding of the structural and functional properties of the neural substrates underlying channel-based duration encoding.

In this dissertation we employ the technique of sensory adaptation to answer several questions about duration-tuned mechanisms and the role they play in duration encoding. The occurrence of the DAE reflects changes in activation in the neural structures responsible for duration encoding. As such, we can use the occurrence, or relative magnitude, of the DAE as a measurement of the activation occurring within duration-tuned neural structures during adaptation. By manipulating experimental condition during adaptation we can measure the effect of these manipulations on the duration encoding process. This allows us to probe the duration encoding process and draw conclusions about the underlying neural structures and their functional properties. In this way, the DAE provides a unique tool that allows us to study the spatial and temporal properties of duration encoding, as well as studying the extraction of duration information from different sources of sensory information under different behavioral circumstances.

In **chapter 2**, we study the relative position of duration-tuned mechanisms along the visual processing hierarchy. The area of visual space over which sensory information is integrated increases along the visual processing hierarchy (A. T. Smith, Singh, Williams, & Greenlee, 2001). As a result, adaptation occurring early on in the visual processing hierarchy leads to after-effects that are restricted to relatively small areas of visual space surrounding the adapted location. In contrast, adaptation occurring at later stages of visual processing leads to after-effects that spread across increasingly larg areas of visual space around the adapted location. We measure the DAE at different adapter-test distances and found no evidence of spatial selectivity for the DAE. From this, we conclude that duration is a feature that is encoded relatively late in the visual processing hierarchy. The fact that the DAE shows no spatial selectivity also established important groundwork for the manipulations/paradigms used in future studies, allowing for spatial manipulations during adaptation which were used in chapter 3 and 4.

In **chapter 3**, we investigate the role of attention in the selective encoding of duration when multiple sources of duration are present. At any given time, we are presented with a large amount of temporal information. This abundance of temporal information requires us to select relevant information to guide our behaviour, while avoiding the influence of irrelevant information. Attention has often been assumed to play an important role in gating duration information for subsequent encoding (Gibbon et al., 1984; Meck, 1984;

Pariyadath & Eagleman, 2007; van Rijn et al., 2014; Zakay & Block, 1997), yet no experimental test of this assumption has been conducted. In the studies reported in this chapter, we use duration adaptation to probe the encoding of attended vs. unattended duration information. During adaptation, observers attend one of two concurrently presented sources of duration information. Next, we measure the relative contribution of attended vs. unattended duration information to the DAE. We demonstrate that observers adapt to attended and not unattended sources of duration information. We conclude that attention plays a crucial role in the selective encoding of duration: attended durations are encoded, while encoding of unattended durations is either weak or absent.

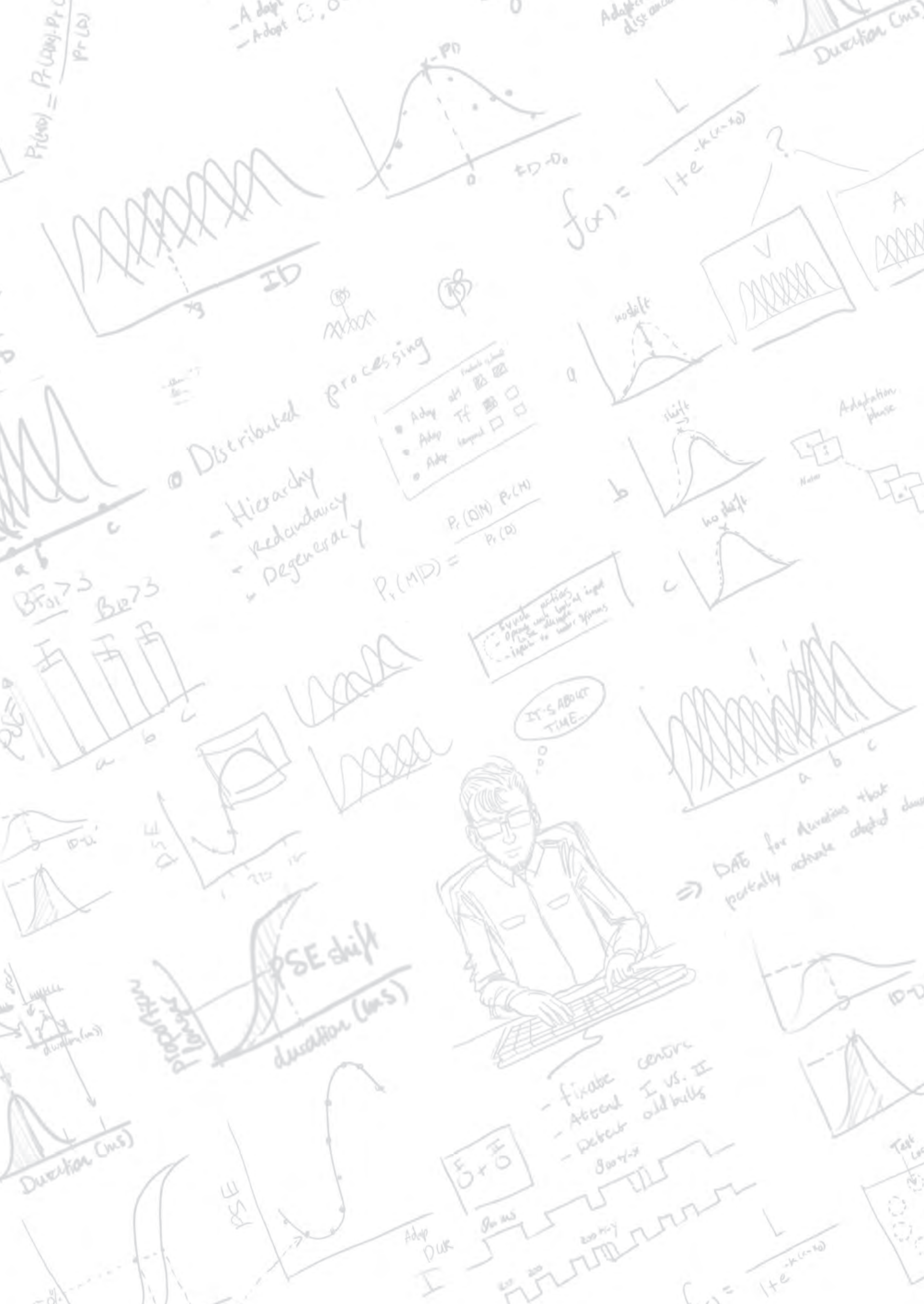
In **chapter 4**, we employ a temporal illusion to investigate the nature of the signal encoded by duration-selective channels. According to the duration channel model, duration is encoded by neurons that respond selectively to the temporal distance between the onset and offset of an event (Heron et al., 2012). This notion is in apparent conflict with the fact that the perceived duration of an event can change, without concurrent changes in the perceived onset and offset of that same event (Johnston, Arnold, & Nishida, 2006; Kaneko & Murakami, 2009). Assuming that duration-tuned mechanisms encode the duration of events, one would expect that the duration encoded by these mechanisms reflects the duration as perceived by the observer. We investigate this apparent conflict by adapting observers to an illusion-inducing stimulus which causes changes in the perceived duration of the stimulus, without any concurrent changes in perceived onset and offset of the stimulus. We measure the DAE following adaptation and find that participants adapted to the 'onset-offset duration' and not the 'perceived duration' of the illusion-inducing stimulus. We conclude that duration encoding relies on the length of the sensory signal and does not necessarily reflect the duration eventually perceived by the observer. Interestingly, this conclusion also suggests that duration-tuned mechanisms do not provide the only source of duration information available to observers. Integration with other sources of duration information or some other additional processing is required to explain the dissociation between the duration encoded by the duration-tuned mechanisms and the duration perceived by the observer.

In sum, these chapters further our understanding of the channel-based encoding of duration and the role that channel-based encoding plays in our perception of duration. Furthermore, our results provide valuable insights for designing future experiments into the nature of duration encoding. The implications of this work, outstanding questions, and future direction are discussed in the general discussion in **chapter 6**.

The perception of temporal frequency

Another important source of temporal information is the rate at which we perceive our world to change. Change informs us of the fact that time is passing and creates recognizable moments in time that allow us to analyze the order and duration of events. Since more time is likely to pass as more things change, change can also inform us about the duration of events. In line with this idea, studies have shown that increasing the rate of change – or temporal frequency – of an event leads to an increase in perceived event duration (Brown, 1995; Herbst, Javadi, van der Meer, & Busch, 2013; Kanai, Paffen, Hogendoorn, & Verstraten, 2006; Linares & Gorea, 2015). This has led researchers to underscore the importance of temporal frequency information for the perception of duration (Brown, 1995; Kanai et al., 2006; Poynter, 1989). More recently, Roseboom and colleagues presented a model in which changes in neural activity in a perceptual classification network as a results of changes in a visual scene can be used to create a system that can reliably encode event time (Roseboom et al., 2017). Together, these studies underscore the relevance of studying temporal frequency processing for our overall aim to understand the processing of temporal information in humans.

In **chapter 5** we used this relationship between temporal frequency content and duration to study the maintenance of temporal information in situations in which this information is no longer present. We used the same temporal illusion as in **chapter 4** and measured the effect of temporal frequency content on perceived duration when the temporal frequency stimulus became occluded. In two experiments, we demonstrate that the (expected) temporal frequency content of an occluded stimulus modulated the duration reported by the observers. From this, we conclude that the representations of occluded objects contain a wide range of features derived from the period when the object is still visible, including information about both the static and dynamic properties of the object. At the same time, our results underscore the role of temporal frequency as an integral part of observers' perception of duration. Even when stimulus information is absent, (predicted) temporal frequency content is still actively maintained and integrated into observers' perception of duration.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Distributed processing
- Hierarchy
- Redundancy
- Degeneracy
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no shift
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Adaptation phase
BF01>3
B10>3
PSE
IT'S ABOUT TIME...
PSE shift
duration (ms)
Proportion longer
DAE for durations that partially activate adapted dura
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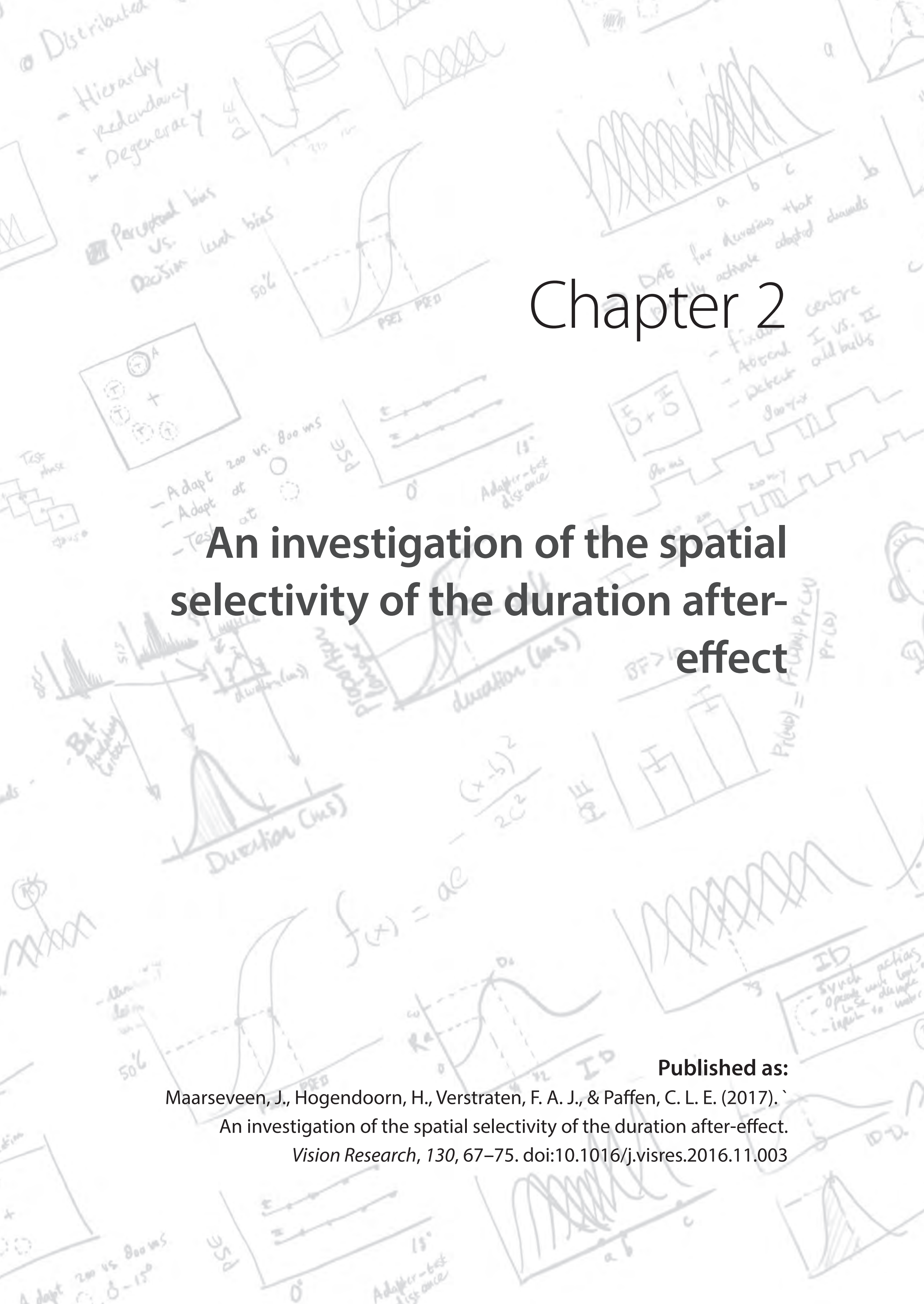

Chapter 2

An investigation of the spatial selectivity of the duration after-effect

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Abstract

Adaptation to the duration of a visual stimulus causes the perceived duration of a subsequently presented stimulus with a slightly different duration to be skewed away from the adapted duration. This pattern of repulsion following adaptation is similar to that observed for other visual properties, such as orientation, and is considered evidence for the involvement of duration-selective mechanisms in duration encoding. Here, we investigated whether the encoding of duration – by duration-selective mechanisms – occurs early on in the visual processing hierarchy. To this end, we investigated the spatial specificity of the duration after-effect in two experiments. We measured the duration after-effect at adapter-test distances ranging between 0 and 15° of visual angle and for within- and between-hemifield presentations. We replicated the duration after-effect: the test stimulus was perceived to have a longer duration following adaptation to a shorter duration, and a shorter duration following adaptation to a longer duration. Importantly, this duration after-effect occurred at all measured distances, with no evidence for a decrease in the magnitude of the after-effect at larger distances or across hemifields. This shows that adaptation to duration does not result from adaptation occurring early on in the visual processing hierarchy. Instead, it seems likely that duration information is a high-level stimulus property that is encoded later on in the visual processing hierarchy.

Introduction

Human observers can readily encode duration information from events that vary in duration, and use that information to guide their behavior (Fraisse, 1984; Gibbon, 1977). Especially in the sub-second range, accurate duration encoding is instrumental for many complex behaviors such as precise motor control (i.e. in activities such as sport and dance), speech recognition and generation, and the processing of social cues (Ambadar, Cohn, & Reed, 2009; Buhusi & Meck, 2005; Diehl, Lotto, & Holt, 2004; Janata & Grafton, 2003; Mauk & Buonomano, 2004; Merchant & Georgopoulos, 2006; Schmidt, Ambadar, & Cohn, 2005). Recently, there has been a renewed interest in studying this temporal aspect of our behavior and the way in which our brain encodes this information. This has resulted in several different types of models on duration encoding that each propose different mechanisms for the encoding of duration (Gibbon, 1977; Ivry & Schlerf, 2008; Jones & Boltz, 1989; Karmarkar & Buonomano, 2007; Matell & Meck, 2004; van Wassenhove, 2009).

A recent model suggests the involvement of duration-selective neurons in the processing of duration information (Becker & Rasmussen, 2007; Heron et al., 2012). Evidence for these models come from adaptation studies that demonstrate a duration after-effect following adaptation. For example, Heron et al. (2012) showed that adapting to the duration of a visual or auditory event causes the perceived duration of a subsequently presented event with a slightly different duration to be skewed away from the adapted duration. This pattern of repulsion following adaptation to duration occurred when both stimuli were of the same modality but not for different modalities, implicating modality specific processing of duration. Importantly, this duration after-effect only occurred when the adaptation duration was close to the tested duration, disappearing when the difference between the two stimuli exceeded ~1.5 octaves. As such, adaptation to duration resulted in a pattern of repulsion similar to that observed for other visual properties such as orientation, spatial frequency, and temporal frequency, which are known to be processed by groups of neurons that show feature selectivity (K. K. De Valois, 1977; R. L. De Valois, Albrecht, & Thorell, 1982; R. A. Smith, 1971). Similar results have been reported by studies investigating the effect of trial history on duration judgments (Becker & Rasmussen, 2007; Walker, Irion, & Gordon, 1981). These studies also show that presentation of a particular duration causes the perception of subsequent shorter or longer durations to shift away from the duration that was presented earlier (Becker & Rasmussen, 2007; Walker et al., 1981). Finally, studies investigating duration discrimination training have shown that training benefits such as increased discrimination sensitivity do not transfer to other non-trained durations (Bartolo & Merchant, 2009; Bueti & Buonomano, 2014; Karmarkar & Buonomano, 2003; Wright et al., 1997). All these studies are consistent with a channel-based model of duration processing in which duration is processed by groups of neurons that selectively respond to specific durations (Hayashi et al., 2015; Heron et al., 2012). Reading out the relative activation of groups of these neurons would allow for an explicit representation of duration that can be used for further processing. The observation that the duration after-effect does not transfer across modalities suggests that duration information is encoded separately for each modality, and combined later on during processing to form a more complete, multimodal representation of duration (Heron et al., 2012, 2013; van Wassenhove, 2009).

A relevant question that is currently being investigated is that of the relative position of these duration-selective channels along the visual processing hierarchy (Hayashi et al., 2015; Heron et al., 2013; Li, Yuan, & Huang, 2015). It has been proposed that duration-selective neurons are present in early sensory areas for both auditory and visual information (Heron et al., 2012). Evidence for this claim comes from single cell recording studies in different mammals that have reported duration-selective neurons in both early auditory processing areas such as inferior colliculus and the auditory midbrain (Brand, Urban, & Grothe, 2000; Casseday, Ehrlich, & Covey, 1994; Ehrlich et al., 1997; He et al., 1997), as well as early visual areas such as area 17 & 18 (Duysens et al., 1996; Eriksson, Tompa, & Roland, 2008). One can argue that an early locus for duration processing can be beneficial given that the temporal integration window of neurons is known to increase along the visual processing hierarchy (Hasson, Yang, Vallines, Heeger, & Rubin, 2008). Therefore, encoding duration information at an early stage of visual processing would potentially allow for more precise encoding of the onset and offset of an event, resulting in more accurate duration encoding. Furthermore, several studies on duration perception have shown that adaptation to both temporal and non-temporal visual features can cause changes in the perceived duration of subsequent events, which are restricted to the location at which adaptation took place (Johnston et al., 2006; Ortega et al., 2012; Zhou, Yang, Mao, & Han, 2014). For example, it has been shown that adapting to the temporal frequency content of a stimulus can cause spatially localized shifts in the perceived duration of subsequent events. These spatially selective after-effects following adaptation have been attributed to modulation in neurons in LGN and V1 (Ayhan, Bruno, Nishida, & Johnston, 2009; Johnston et al., 2006; Ortega et al., 2012; but see Burr, Tozzi, & Morrone, 2007; Fornaciai, Arrighi, & Burr, 2016). These findings suggest a strong relation between low-level visual processing and the encoding of temporal information.

The above studies suggest that duration information is processed at early levels of processing. However, behavioral studies have shown that trial history effects and the duration after-effect do not show any selectivity to low-level visual features such as orientation (Li, Yuan, & Huang, 2015; Walker et al., 1981), arguing against a role of early visual cortex in channel-based duration processing. Furthermore, many other different brain areas have been implicated in duration processing, providing alternative possible neural loci for the channel-based encoding of duration (Hayashi et al., 2015; Ivry & Schlerf, 2008; Mauk & Buonomano, 2004). For example, single cell recordings in macaques have revealed duration selectivity in striatal neurons (Mello, Soares, & Paton, 2015) as well as in the pre-supplementary motor area (pre-SMA) (Merchant, Pérez, et al., 2013). More recently, Hayashi et al. (2015)investigated single duration repetitions in humans using fMRI. They showed a decrease in BOLD response in the right-supramarginal gyrus (r-SMG) when the duration of a stimulus was similar to a previously presented stimulus, as compared to when both were dissimilar. This suppressed response to repetition was replicated for several different intervals and did not seem to be the result of a general similarity judgment, only occurring for duration judgments (Hayashi et al., 2015).

In sum, it is clear that the mechanisms involved in duration processing and their related structures in the human brain are yet to be established. The goal of this study was to further investigate the relative position of duration-selective mechanisms along the visual processing hierarchy by investigating the spatial selectivity of the duration after-effect. It is well known that the spatial scale over which sensory information is integrated increases along the visual processing hierarchy (A. T. Smith et al., 2001). This is the result of differences in receptive field size of individual neurons in different cortical areas. For early visual areas such as V1, receptive fields have been found to be as small as 0.5°, with the estimate receptive field size steadily increasing along the visual processing hierarchy (Amano, Wandell, & et al., 2009; Dumoulin & Wandell, 2008; Harvey & Dumoulin, 2011; A. T. Smith et al., 2001). This characteristic has often been used to dissociate between processes occurring at different levels of the visual processing hierarchy. For example, in the domain of visual motion processing this has been used to dissociate between motion after-effects occurring in V1 and those occurring later in processing in areas MT (Kohn & Movshon, 2003). Applying this type of paradigm will allow us to make similar distinctions for the mechanisms involved in the encoding of duration information. If the encoding of duration – by duration-selective mechanisms – occurs early in the visual processing hierarchy, the duration after-effect should be restricted to within a few degrees of visual angle from the adapted location. Conversely, if duration information is encoded later on in the visual processing hierarchy, the duration after-effect should remain relatively constant across visual space.

Here, we present two experiments investigating the spatial selectivity of the duration after-effect by parametrically varying the distance between adaptation and test stimulus. We adopted the paradigm introduced by Heron et al. (2012, 2013) and adapted participants to visual stimuli of varying duration. Following adaptation, participants completed a cross-modal duration judgment task comparing an auditory reference to a visual test stimulus. To evaluate the effect of visual distance on the duration after-effect, test stimuli were placed at a range of distances from the adapted location. In a second experiment, we further explore the impact of visual and cortical distance on the duration after-effect by measuring the duration after-effect for both within- and between-hemifield presentations.

Experiment 1

Method

Participants. Nine participants completed the experiment (1 male, M_{age} = 20.91 *SD* = 3.02). All participants had normal or corrected-to-normal vision and were naïve as to the purpose of the experiment. Before the experiment all participants gave written informed consent. After completing the experiment, participants received a monetary reward or course credits. The experiment was conducted in line with the principles expressed in the Declaration of Helsinki and received approval by the Local Ethics Committee

Materials and stimuli. All visual stimuli were presented on a linearized 22-inch CRT monitor (screen resolution at 1024 x 768 pixels, 100 Hz refresh rate) controlled by an Apple Mac Mini. Participants viewed the screen from a distance of 57 cm. Head movement was restrained using a chinrest.

The stimulus display consisted of a white central fixation cross (64.1 cd/m^2; 0.40 x 0.40°) presented on a gray background (8.28 cd/m^2). All visual stimuli were Gaussian blobs ($r = 0.75°$, 76% peak Michelson contrast) presented at 8° from the center of the screen. The auditory stimuli consisted of bursts of white noise (65.4 dB) presented through a Sennheiser HD201 on ear headset. In a pilot study, we found that the relation between the perceived duration of auditory and visual stimuli varied considerably between participants. To assure that the visual presentation was similar for each participant, we set the auditory reference duration to be perceived as equal to a 320 ms visual stimulus. Participants completed a cross-modal duration judgment task in which the auditory reference duration was varied using an Accelerated Stochastic Approximation (ASA) staircase procedure (Kesten, 1958). This resulted in an average auditory reference duration of 321.14 ms (*SD* = 66.73). All stimuli were generated and presented using MATLAB 2015b (MathWorks, Inc.) and the Psychophysics Toolbox 3.0.12 (Brainard, 1997; Pelli, 1997). All timings were verified using a dual channel oscilloscope.

Procedure. In separate blocks, participants adapted to 100 repetitions of a visual stimulus lasting either 160 ms or 640 ms. The adaptation stimulus was always presented directly above the fixation cross at a distance of 8° of visual angle. To avoid clear temporal patterns or adaptation to on-off temporal frequency the inter-stimulus interval (ISI) was varied randomly between 500 and 750 ms. During the adaption phase, the participants' task was to maintain central fixation while attending the repetitions of the adaption stimulus. Following the adaptation phase the text "duration judgment phase" appeared for 2 s to inform the participants that they had entered the test phase.

Each trial of the test phase started with 4 top-up repetitions of the adaptation stimulus followed by a cross modal duration judgment task. For this task participants were instructed to compare the duration of an auditory reference tone to that of a visual test stimulus presented randomly at one of five possible adapter-test distances (center to center distance: 0, 6, 8, 11, 15°). For each distance, the location of the test stimulus was varied randomly between left and right of the fixation cross. The duration of the test stimulus was varied using the Minimum Expected Entropy staircase method (Saunders & Backus, 2006). Participants reported their judgment by pressing either the left ('sound longer') or right ('visual longer') arrow key. After reporting their judgment the next test trial was initiated after a 500 ms delay. An overview of both phases can be found in Figure. 1.

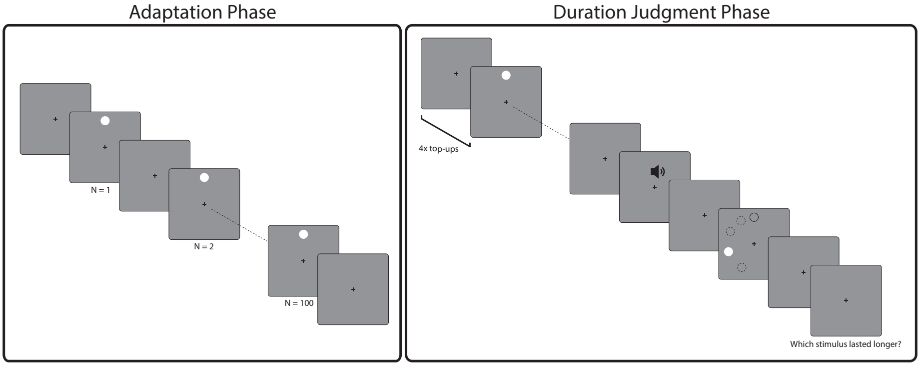


Figure 1. Schematic representation of a single adaptation block. Each block started with an Adaptation Phase (left) in which participants were presented with a 100 repetitions of the adaptation stimulus (160, 640 ms) presented 8° above central fixation. In the following Duration Judgment Phase, participants were presented with 4 repetitions of the adaptation stimulus (top-up) followed by a cross-modal duration judgment task (right). In this task, they compared an auditory reference to a visual test stimulus presented at one of the 5 possible test locations. The dashed line annuli only serve to illustrate the alternative locations of the test stimulus and were not actually shown on the screen.

After completing 40 trials participants were informed on their progress ("Block x of 10") and were allowed to take a short self-timed break. Participants completed 10 blocks and a total of 400 trials. This equates to 40 trials for each unique combination of conditions. All measurements were conducted over two 50-min sessions separated by a 15-min break.

Results & discussion

We calculated the point of subjective equality (PSE) based on the psychometric function estimated by the Minimum Expected Entropy staircase for each condition, for each participant. These data can be found in the Supplementary materials (Figure S1). Next, we calculated the average PSE for each of the 10 conditions (Figure 2). This data was then subjected to a 2 x 5 repeated-measures ANOVA with PSE as the dependent measure and Adaptation Duration and

Distance as independent measures. All tests were evaluated at alpha = 0.05. Post-hoc comparisons were adjusted for multiple comparisons using the Holm-Bonferroni correction method (Holm, 1979). The error bars in all images reflect within-subject variability, calculated using per-subject normalization of the data (Cousineau, 2005; Morey, 2008).

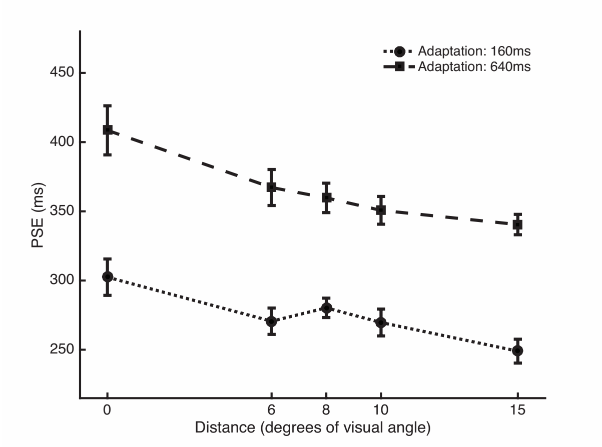


Figure 2. Average PSEs for the 160 and 640 adaptation durations are plotted as a function of adapter-test distance. Higher PSEs reflect a shorter perceived duration of the test stimulus.

The results reveal a main effect of Adaptation Duration (*F*(1,8) = 46,49, $p < 0.001$, $\eta^2 = 0.85$) with lower PSE estimates following adaptation to a 160ms stimulus compared to adaptation to a 640 ms stimulus. In other words, adaptation to a longer duration resulted in a shorter perceived duration for the test stimuli compared to adaptation to a shorter duration. In addition, we found a main effect of Distance (*F*(4,32) = 8.72, $p < 0.001$, $\eta^2 = 0.52$), reflecting a general decrease in PSE for higher distances indicating an increase in perceived duration with increasing adapter-test distance. Subsequent paired sample t-tests for the main effect of Distance revealed that the PSE was significantly higher when the test stimulus was present at the same location as the adapter stimulus (0°) compared to an adapter-test distance of 15° (*t*(8) = -4.99, $p < 0.001$). No other comparisons reached statistical significance (all $p > 0.064$). We also analyzed the slope for the main effect of Distance by calculating the mean PSEs across the two Adaptation Durations for each participant followed by a linear regression. We then conducted a simple *t*-test and found that the slope was significantly lower than zero (*t*(8) = 4.80, $p < 0.001$).

Importantly, we found no evidence for a significant interaction between Adaptation Duration and Distance (*F*(4,32) = 0.75, *p* = 0.567, $\eta^2 = 0.09$) indicating that the effect of Adaptation duration did not significantly change across the different adapter-test distances. To underpin this finding, we conducted an additional Bayesian analysis using JASP (Love et al., 2015) to evaluate the likelihood that the magnitude of the duration after-effect was constant across all measured distances. First, we calculated the magnitude of the duration after-effect by subtracting the PSEs for the 640 ms Duration adaptation conditions from those of the 160 ms Duration Adaptation conditions (Figure 3). The resulting score, which reflected the magnitude of the duration after-effect, was then further analyzed using a Bayesian repeated-measures ANOVA with Duration After-effect as a dependent variable and Distance as an independent measure. This analysis revealed that the data was almost five times more likely to reflect a null effect compared to the alternative hypothesis of a significant change in the duration after-effect across adapter-test distance (BF01 = 4.74).

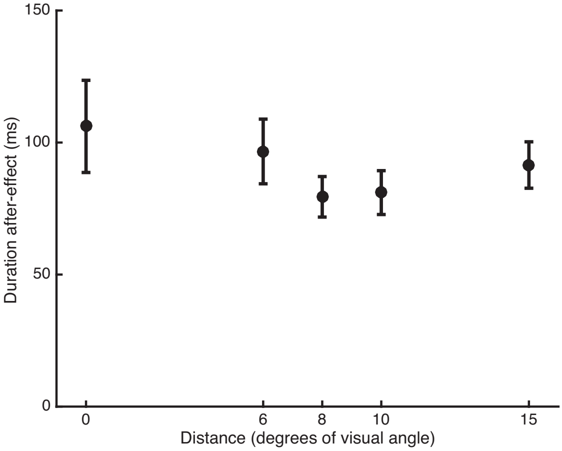


Figure 3. Magnitude of the duration after-effect as a function of adapter-test distance. The magnitude of the adaptation after-effects is calculated by subtracting the PSEs for the 640 ms Duration adaptation conditions from those of the 160 ms Duration Adaptation conditions.

We observed a clear duration after-effect, corroborating the findings by Heron and colleagues (2012, 2013). More importantly, the effect of adaptation was present at each of the measured distances and did not decrease for larger adapter-test distances. This result indicates that the duration after-effect does not show the spatial selectivity that would be expected if the duration-selective mechanisms were located early on in the visual processing hierarchy. Instead, it seems more likely that the channel-based encoding of duration occurs further upstream in the visual processing hierarchy, where receptive fields are not confined to relatively small areas of visual space.

Experiment 2

Given the distances used in Experiment 1, it seems likely that the neuronal mechanisms responsible for channel-based duration processing of visual information have relatively large receptive fields, arguing against a role for low-level visual processing areas in duration perception. To further explore this notion, we investigated the hemifield specificity of the duration after-effect.

Due to the anatomical separation between hemispheres, the degree of interhemispheric transfer of visual information is different at different levels of processing. As a result, there is no direct interhemispheric integration in early visual areas, with the amount of interhemispheric integration increasing along the visual processing hierarchy. This anatomical property has functional consequences for the processing of information presented in different hemifields. For lower-visual areas (V1-4) responses are strongly restricted to stimulation in the contralateral visual field, extending no more than 3–4° into the ipsilateral field (Amano et al., 2009; Gattass, Gross, & Sandell, 1981; Gattass, Sousa, & Gross, 1988; Winawer, Horiguchi, Sayres, Amano, & Wandell, 2010). For other areas receptive fields show much larger responses to stimulation in the ipsilateral visual field (Amano et al., 2009). However, the response to ipsilateral stimulation is often found to be weaker due to large amount of feedforward input stemming from lower-level visual neurons that only respond to stimulation in the contralateral field (Ffytche, Howseman, Edwards, Sandeman, & Zeki, 2000; Huk, Dougherty, & Heeger, 2002). One example of the functional consequences of cortical separation is the fact that adaptation to numerosity – believed to originate in parietal areas of the brain (Harvey et al., 2013) – has been shown to transfer across visual space, but not visual hemifield (Burr & Ross, 2008; Choo & Franconeri, 2010). While parietal areas have relatively large receptive fields – as well as areas that do not show any form of retinotopic mapping – crossing into the opposite hemifield reduces the magnitude of the numerosity after-effect. Beyond cortical distances there are other difference between intra- and inter-hemispheric processing. One example of this is the observation that subjects can track twice as many items when they are presented in separate hemifields, compared to when they are presented in the same hemifield. This finding points towards the existence of separate attentional networks for each hemisphere (Alvarez & Cavanagh, 2005; Cavanagh & Alvarez, 2005). As such, hemifield specificity of the duration after-effect could be considered another case of spatial specificity. Alternatively, it could reflect a form of lateralization related to separate attentional processing.

Because the adaptation stimuli in Experiment 1 were always presented on the vertical midline, we could no evaluate the possibility of hemifield specific processing. To address this, we conducted a second experiment in which the duration after-effect was evaluated at two different adapter-test distances with the largest distance falling either within- or between-hemifields. If adaptation to duration occurs only within the adapted hemifield, we would expect the duration after-effect to disappear for test stimuli presented in the opposite hemifield. We also addressed a possible issue in experiment one, where we did not control for any eye-movements and changes in gaze position. Given the large number of adaptation repetitions and the salience of test stimuli presented away from the adapted location, it is possible that participants did not strictly maintain central fixation throughout the experiment. Fixating on adaptation, top-up, or test stimuli while they are being presented would inflate the maximum distance at which the after-effect could be observed. More problematically, fixating both adaptation and test stimuli would lead to a duration after-effect that appears to 'transfer' across spatial distance, while simply reflecting adaptation measured at a distance of ~0 degrees of visual angle. To control for this issue, we measured gaze-position throughout the experiment.

Method

Participants. Sixteen participants completed the experiment (4 male, M_{age} = 25.00, *SD* = 4.57). All participants had normal or corrected-to-normal vision and were naïve to the purpose of the experiment. Before the experiment, all participants gave written informed consent. After completing the experiment, participants received a monetary reward or course credits. The experiment was conducted in line with the principles expressed in the Declaration of Helsinki and received approval by the Local Ethical Committee. For half of the participants (N=8) we measured gaze position throughout the experiment.

Materials and stimuli. For the non-eyetracking runs of the experiment, materials were the same as in Experiment 1 & 2. For the runs including eyetracking, a different setup was used to accommodate the use of our eye-tracker. Stimuli were presented on the same monitor but were controlled by a Dell OptiPlex 7040 workstation running Windows 10 and Matlab 2015b. Display luminance for all stimuli was matched for both setups, with all deviations <0.05 cd/m^2. Average luminance values are reported for this experiment. All timings were evaluated using a dual channel oscilloscope. Gaze position was measured using an EYE TRIBE tracker sampling at 30 Hz, controlled using the PyGaze software package and eye tribe toolbox for Matlab (Dalmaijer, 2014; Dalmaijer et al., 2014). Finally, we used a chin- and headrest, to increase head stability.

All stimuli were equal to those used in Experiment 1 (Gaussian blob: r = 0.75°, 76% peak Michelson contrast) and were accompanied by a central fixation dot (64.2 cd/m^2; 0.50 x 0.50°) presented on a gray background (8.29 cd/m^2). Once more, an ASA staircase procedure was used to set the duration of the auditory stimulus (M = 291.29 ms, SD = 57.87 ms). All other presentation conditions and timings were identical to experiment 1.

Procedure. The procedure was similar to that of the first experiment. Participants adapted to a 100 repetitions of a visual stimulus lasting 160 ms or 640 ms. All stimuli were presented 8° from the center of the screen at 4 different possible angles (45, 135, 225, and 315 degrees; see Figure 4). The location of the adaptation stimuli was counterbalanced across these 4 locations, with a single location being used for each participant. For each participants test stimuli were always presented at one of three possible locations: At the adapted location, in the horizontally adjacent quadrant, or in the vertically adjacent quadrant. This resulted in two adapter-test distances (center-to-center distance: 0, 11.31°), with the non-zero distance being presented either within- or between-hemifield (Figure 4).

For the eyetracking group, the procedure was expanded to include gaze measurements. At the start of each experiment we tested the fidelity of the gaze signal by running two test 9-point calibrations. In case the eyetracking signal was too poor to complete calibration, another unrelated experiment was conducted instead. Three people were excluded via this procedure. After this initial check, we started the experiment. At the start of each block, participants were (re)calibrated to assure good calibration. Additionally, at the start of each trial an automated drift check was conducted, continuing after participants had successfully fixated within 2° of the center of the fixation dot for 250 ms. If participants failed the automated drift check, the eye tracker was recalibrated. Gaze position was monitored throughout both the adaptation and test phase. Additionally, presentation of the test stimulus was gaze contingent, with failed fixation (deviation >2°) leading to a disappearance of the test stimulus and re-run of the same trial. In total, participants completed 6 blocks each containing 50 trials (300 trials total). This equated to 50 trials for each unique combination of conditions. All measurements were conducted across two 50-min sessions separated by a 15-min break.

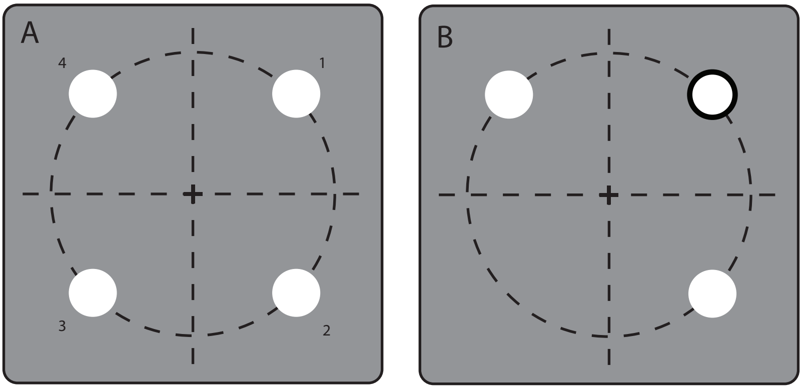


Figure 4. Schematic representation of the stimulus display in Experiment 3 (dotted lines for illustrative purposes only). A) For each participant adaptation stimuli were presented at one of the 4 positions. Test stimuli were presented at either the same location, or in the adjacent horizontal and vertical quadrants. This led to three possible presentation conditions: same locations (0°), within-hemifield (11.31°) or between-hemifield (11.31°). B) An example display for a single participant, the outlined circle indicates the adapted location and the white circles show possible test locations.

Results & discussion

Eyetracking data. The eyetracking signal was stable throughout most of the experiment with only a small percentage of missed samples during stimulus presentation: adaptation presentations (3.94%), top-up presentations (5.42%), and test stimulus presentation (0%). We analyzed the successfully measured samples by calculating the percentage of fixations that fell within 2 degrees of visual angle from the central fixation dot. We found that participants fixated the fixation dot 97.03% (SD: 1.10%) of the time during the presentation of adaptation stimuli, 96.25% (SD: 1.66%) of the time during top-up presentation, 99.79% (SD: 0.28) of the time during the presentation of the test stimulus.

Additionally, we looked at the percentage of trials that was canceled due to the loss of fixation during the presentation of the test stimulus. On average this occurred on 1.70% (SD: 2.54) of the trials. Together these data show that participants were able to follow instruction and maintain fixation throughout the experiment.

Behavioral data. We calculated the point of subjective equality (PSE) based on the psychometric function estimated by the Minimum Expected Entropy staircase for each condition, for each participant (Figure S2). Average PSEs for each of the 9 conditions can be found in Figure 5. This data was then subjected to a 3 x 3 ANOVA with PSE as the dependent measure and Adaptation Duration (160, 640ms) and Locations (0°, 11.31° Within, 11.31° Between) as within-subject factors.

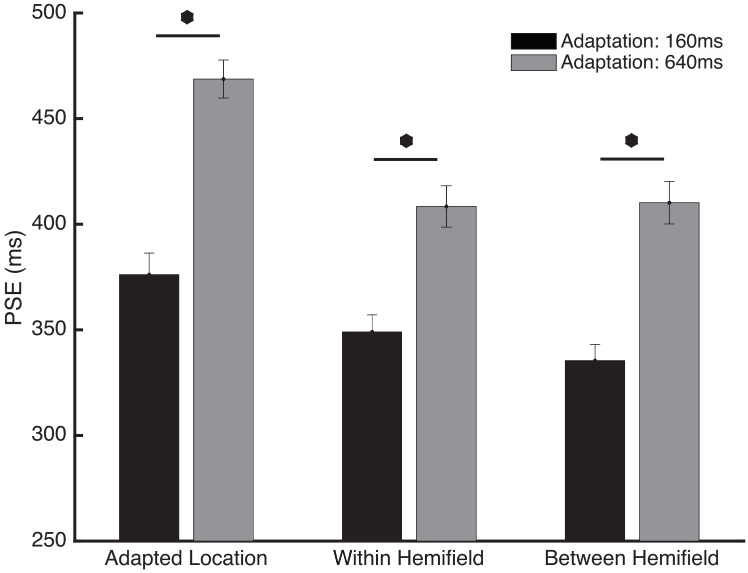


Figure 5. Average PSEs for the 160 and 640 ms adaptation durations plotted for each of the three test locations.

We again found a main effect for Adaptation Duration ($F(1,15) = 48.93$, $p < 0.001$, $\eta^2 = 0.77$), replicating the duration after-effect reported in experiment 1. We also observed a main effect for Location ($F(2,30) = 22.85$, $p < 0.001$, $\eta^2 = 0.604$). Paired sample *t*-test for the main effect of Location reveal a significantly shorter perceived duration for the 0° distance presentations compared to both non-zero distance presentations (both $p < 0.001$). No significant difference between the between- and within-hemifield presentations was observed ($t(15) = 0.64$, $p < 0.53$). Importantly, we found no evidence for an interaction between Adaptation Duration and Location ($F(2,75) = 2.34$, $p < 0.114$, $\eta^2 = 0.0.135$). A Bayesian repeated measure ANOVA with Magnitude of the Duration After-effect as a dependent variable and Distance as an independent measure revealed no clear evidence for either the null hypotheses or alternative hypothesis (BF01=1.23), indicating uncertainty about whether the duration after-effect varied across the different adapter-test locations. Visual inspection of the magnitude of the duration after-effect for each of the three Location conditions shows that the after-effect is numerically highest for presentation at the adapted location and lowest at the within-hemifield location. As such it is unlikely that this uncertainty reflects evidence for a smaller after-effect for between-hemifield presentations.

In Experiment 2, we replicated the results from Experiment 1, demonstrating a clear duration after-effect at all measured locations. We also replicated the general increase in perceived duration for increasing adapter-test distances observed in Experiment 1. More relevant to answering our question, we found no evidence for a decrease in the magnitude of the duration after-effect at a distance of 11.31° for both within- and between-hemifield presentations. Additionally, we demonstrate that our findings cannot be explained by a failure to fixate during presentation of the adaption or test stimuli.

General discussion

The goal of this study was to investigate the relative position of duration-selective mechanism along the visual processing hierarchy. More specifically, we aimed to evaluate the possibility that the duration after-effect originates from duration-selective mechanisms that are located in early visual areas, as has previously been suggested (Heron et al., 2012). To address this issue we investigated the spatial selectivity of the duration after-effect by parametrically varying the distance between adapter and test stimuli in two experiments. In both experiments we observed a duration after-effect, replicating the pattern of repulsion following duration adaptation demonstrated in earlier studies (Heron et al., 2012, 2013; Li, Yuan, & Huang, 2015). Furthermore, the duration after-effect occurred at all measured distances, with no evidence for a decrease in the magnitude of the after-effect at larger distances. In Experiment 2 we investigated the possibility of hemifield specificity for the duration after-effect. We observed similar results for both within- and between-hemifield adaptation to duration, with no evidence for any hemifield specificity. Finally, we demonstrate that the effects observed in our study are not the result of fixating adaptation/test stimuli during the experiment.

In these experiments we observed a duration after-effect that transfers over distances up to 15°, as well as transfers to locations in the hemifield opposite to the adapted location. From these findings we conclude that it is unlikely that the duration after-effect originates from adaptation in early visual areas as has originally been proposed. This conclusion is further supported by recent work reporting transfer across hemifields following adaptation to duration (Li, Yuan, Chen, Liu, & Huang, 2015). In their experiment, the duration after-effect was assessed for two locations located in opposite hemifields, confounding distance and hemifield. The findings reported here corroborate their finding as well as providing an independent, parametric measurement of the duration after-effect across visual space as well as between hemifields.

To provide a more descriptive discussion about the transfer across different adapter-test distances and its relation to retinotopically mapped visual areas we can compare our data to population receptive field size estimates from human fMRI data. It is important to note that receptive field size in these studies is expressed as the sigma of the Gaussian describing the receptive field. Calculating the full-width-half-max for these Gaussians increases its size by a factor of ~2.35. For early visual areas such as V1-3, estimated population receptive field size at an eccentricity of 8° ranges from 2° to 4° (Amano et al., 2009; Harvey & Dumoulin, 2011; Zuiderbaan, Harvey, & Dumoulin, 2012). As such it is very unlikely that adaptation in these areas underlie the duration after-effect reported here. For later visual areas such as V4, lateral occipital cortex (LO), and middle temporal visual areas (MT/MST), these estimates are much larger (6–14°) (Amano et al., 2009; Harvey & Dumoulin, 2011; Winawer et al., 2010). This relatively large size (FWHM: ~14.1–32.9°) makes it more difficult to exclude these areas based on the distances measured here. When looking at visual field maps and their responsiveness across hemifields, a similar but complementary image emerges. For early visual areas (V1-4) response are strongly restricted to information in the contralateral visual field, extending no more than 3–4° into the ipsilateral field (Amano et al., 2009; Winawer et al., 2010). This corroborates our earlier statement about V1-3 and includes V4 as an unlikely candidate based on our between hemifield data. For later visual areas receptive fields extend into the ipsilateral visual field to a large extent (Amano et al., 2009). However, response to ipsilateral stimulation for areas such as V5 is often weaker compared to responses to contralateral stimulation due to the abundance of feed-forward input from lower-level neurons that only respond to stimulation in the contralateral field (Ffytche et al., 2000; Huk et al., 2002). This property has been used to dissociate related areas such as MT and MST (Ffytche et al., 2000; Huk et al., 2002). Based on these findings one might predict some decrease in the duration after-effect for between hemifield presentations for areas such as MT. Our current results did not show any significant decrease in the magnitude of the duration after-effect. However, one could argue that a numerical decrease is apparent for the non-zero conditions in our second experiment. As such, we should be careful in making strong claims about the involvement of areas that have large receptive fields, such as MT, based on the data and adapter-test distances used in our experiments. To further dissociate the involvement of higher visual areas with large receptive fields (MT, LO, TO) in the encoding of duration, it would be more appropriate to use other experimental methods that focus on specificity based on visual features that are relevant to these 'middle/higher-level' areas (i.e. motion direction selectivity for V5). For now, we conclude that areas V1-V4 are unlikely to play a role in duration-selective processing as measured by the duration after-effect reported here. Instead the data suggests that duration-selective processing occurs at later stages of the visual processing hierarchy in visual areas with relatively large receptive fields, or in areas that do not show any spatial sensitivity.

Several studies support the idea of an involvement of higher-level visual areas in the encoding of duration. For example, recent work using single cell recordings and fMRI have reported duration-selective responses in different cortical areas. These areas included the r-SMG (Hayashi et al., 2015), medial premotor cortex (Merchant, Pérez, et al., 2013), and the striatum (Mello et al., 2015). As of now it is unclear what the exact role of these different areas is in the encoding of duration information. Several authors have suggested the possibility that duration is first encoded in a modality specific manner before being combined into a single duration code used for further processing (Heron et al., 2012, 2013; van Wassenhove, 2009). As such, the duration selectivity in different brain areas might reflect further processing of duration information and the application of that information for other processes such as the temporal aspects of motor preparation and cognitive control (Coull et al., 2013; van Wassenhove, 2009).

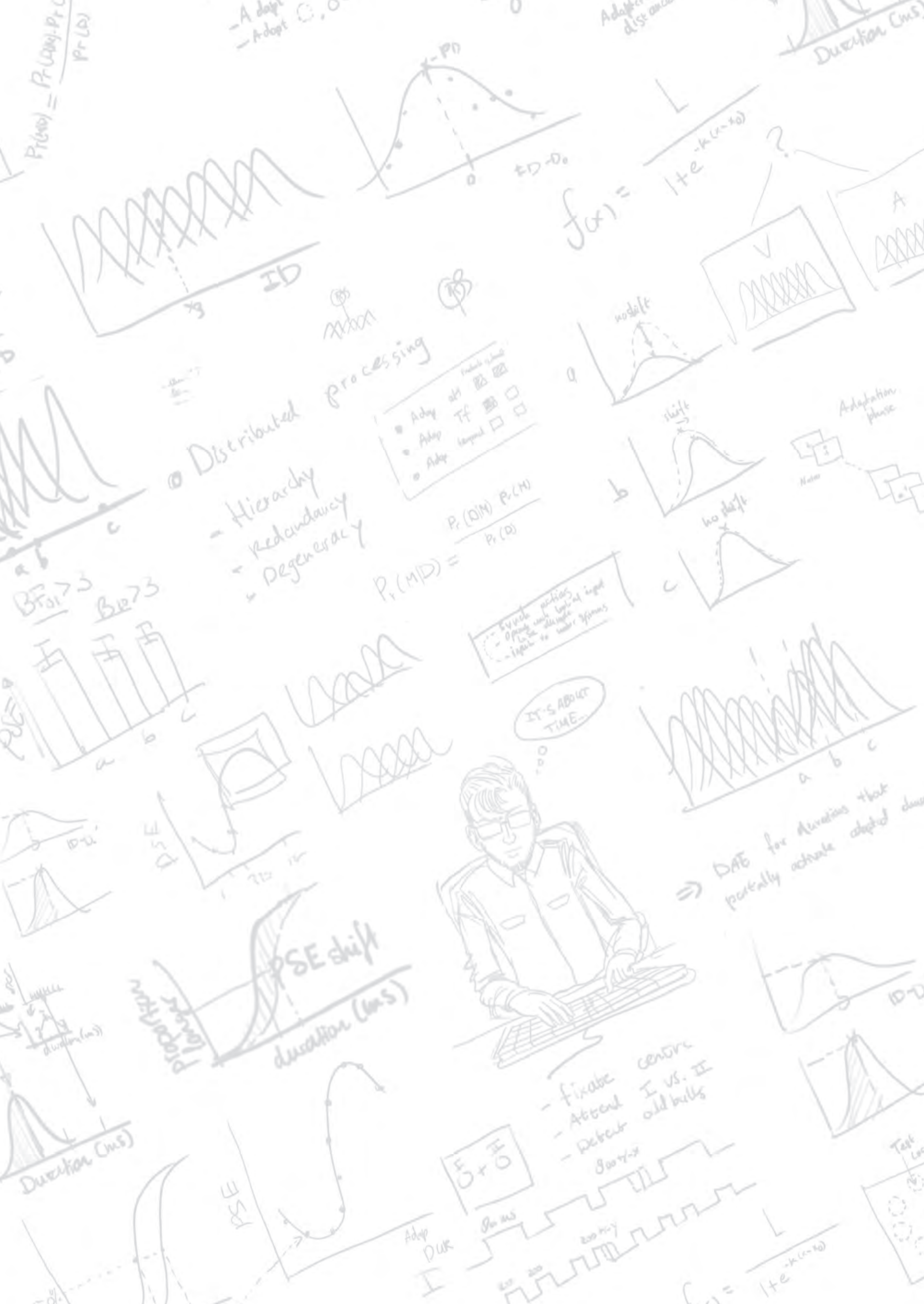
In both of our experiments, we observed that the perceived duration of events increased as the distance from the adapted location increased. One possible explanation for these results is the adaptation to low-level visual stimulus properties (such as luminance, contrast, or spatial frequency) that occur for the 0° distance presentations. Previous studies have shown that adaptation to low-level visual features can cause compression in perceived duration and that these effects are spatially localized to about 2–4 degrees of visual angle (Zhou et al., 2014). As such, adaptation to low-level visual features could explain the increase in perceived duration for the stimuli presented at the non-zero distances. However, this would predict a steep decline between the 0° and all non-zero adapter-test distances, but not the general increase across distance observed in Experiment 1. Alternatively, the decrease observed in Experiment 1 could be due to the fact that adapter-test distance was confounded with vertical position. We controlled for this issue in Experiment 2 by counterbalancing the adaptation location but observed a similar pattern of decreasing perceived duration with adapter-test distance. Another possibility is that the general increase in perceived duration at increasing adapter-test distance could be the result of inhibition of return at the location of the adaptation stimulus. Inhibition of return (IOR) occurs when attention is drawn to a location in visual space that has been recently attended (i.e. in the previous 300–3000 ms; Klein, 2000; Samuel & Kat, 2003). IOR has been shown to have a spatial gradient, being strongest at the attended location and decreasing in magnitude with visual distance (Bennett & Pratt, 2001). Earlier studies on duration perception have shown that attended stimuli are perceived as having a longer duration compared to unattended stimuli or stimuli that receive less attention (Block, Hancock, & Zakay, 2010; Tse, Intriligator, Rivest, & Cavanagh, 2004; Ulrich, Nitschke, & Rammsayer, 2006). In our study, participants were presented with four top-up stimuli at the adapted location followed by the cross-modal duration judgment task, with the visual test stimulus being presented between 1000 and 2000 ms after the last top-up. As such, IOR at the location of the adaptation stimulus could explain the graded increase in perceived duration over visual space.

In the current study, we did not find any evidence for a decrease in the duration after-effect with increased adapter-test distance. While this indicates a strong role for later visuals areas, it does not fully exclude a role for earlier areas. Many adaptation after-effects for more complex stimulus properties (i.e. motion, numerosity, faces) with processing loci in higher-level areas have been shown to also include a low-level adaptation component (Afraz & Cavanagh, 2008; Kovács et al., 2005, 2007). One classic example is the contribution of adaptation in V1 in motion after-effects adaptation (Kohn & Movshon, 2003). The fact that we do not find any evidence for such a lower-level contribution in the duration after-effect might reflect a lack of sensitivity in the method deployed in this experiment. Incorporating neuroscientific methods such as fMRI might provide a more appropriate way to address this question. Despite this nuance about a lower-level contribution, it is safe to conclude that the main locus for duration encoding lies outside earlier visual areas.

The results reported here are in strong contrast with the result of studies investigating the effect of adaptation to other temporal and non-temporal stimulus features on perceived duration (Johnston et al., 2006; Ortega et al., 2012; Zhou et al., 2014). In general, these studies report strong spatial selectivity indicating an origin in early visual areas (e.g. LGN, V1). This suggests that the after-effects reported by these studies and the duration after-effect result from distinct mechanisms located at different stages of visual processing. This, however, raises the question of why distinct mechanisms exist. One answer to this question is to assume a hierarchical structure to the processing of duration (Heron et al., 2013; van Wassenhove, 2009). Models proposing such a structure focus on the idea that temporal information is intrinsically present in any sensory signal (Buonomano, 2000; Buonomano & Maass, 2009; Karmarkar & Buonomano, 2007; van Wassenhove, 2009). These patterns of different states of the network can then be extracted to form a more explicit duration code (e.g. via channel-based encoding) so that it can be integrated across the senses. The resulting multimodal representation can then be stored and interact with other information to inform subsequent behavior. Assuming that the different after-effects reflect different hierarchical steps in duration processing could explain the observed differences in spatial selectivity of these after-effects. We would suggest that adaptation to temporal frequency and non-temporal factors occurs earlier in duration processing by causing modulations in the states of the network. The duration-selective mechanisms then act upon these (modulated) states to explicitly encode duration. In other words, the different after-effects might not reflect the existence of distinct mechanisms that independently encode duration, but distinct steps in the hierarchal processing of duration.

The observed lack of spatial selectivity for the duration after-effect raises several questions about the selection and simultaneous processing of multiple events with different durations. During natural situations many different events can occur at once leading to an overlap in the durations of different events. However, if duration information from multiple sources cannot be dissociated based on their spatial location, it is unclear how the duration processing mechanisms deal with the presentation of multiple durations. One possibility is that attentional selection plays a role in the processing of multiple durations. A study by Cheng, Yang, Han, Ding, and Fan (2014) showed that human observers are able to process up to four multiple durations at once. Furthermore, duration tracking performance dropped steadily when attention had to be spread over a larger amount of different duration stimuli. This suggests that the processing of duration information from multiple sources relies on attentional selection to bind duration information to specific objects or spatial locations.

To summarize, we found a clear duration after-effect at all measured adapter-test distances. There was no evidence for a decrease in the magnitude of the duration after-effect at larger visual distances or across hemifields. We conclude that the duration after-effect does not result from adaptation occurring early on in the visual processing hierarchy. Instead, it seems likely that duration information is a high-level stimulus property that is encoded later on in the visual processing hierarchy.


Distributed processing
- Hierarchy
- Redundancy
- Degeneracy
IT'S ABOUT TIME...
no shift
shift
no shift
Adaptation phase
PSE shift
duration (ms)
Proportion longer
PSE
Duration (ms)
a
b
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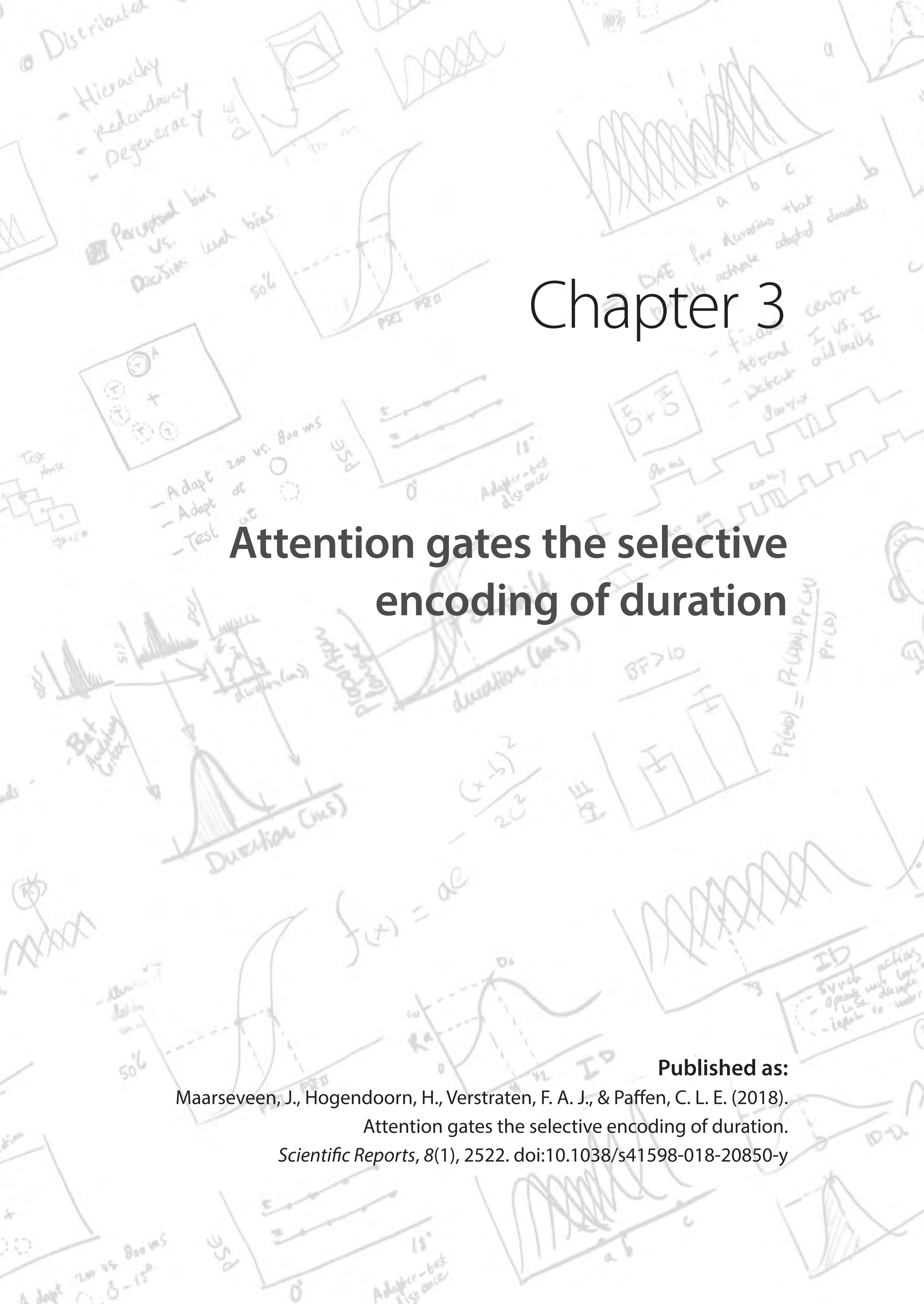
ID
=> DAE for durations that partially activate adapted dur
- fixate centre
- Attend I vs. II
- Detect oddballs
Adap DUR



Chapter 3

Attention gates the selective encoding of duration

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Abstract

The abundance of temporal information in our environment calls for the effective selection and utilization of temporal information that is relevant for our behavior. Here we investigated whether visual attention gates the selective encoding of relevant duration information when multiple sources of duration information are present. We probed the encoding of duration by using a duration-adaptation paradigm. Participants adapted to two concurrently presented streams of stimuli with different durations, while detecting oddballs in one of the streams. We measured the resulting duration after-effect (DAE) and found that the DAE reflects stronger relative adaptation to attended durations, compared to unattended durations. Additionally, we demonstrate that unattended durations do not contribute to the measured DAE. These results suggest that attention plays a crucial role in the selective encoding of duration: attended durations are encoded, while encoding of unattended durations is either weak or absent.

Introduction

Temporal information is crucial to our interaction with the external world. Analyzing the temporal order and duration of events allows us to learn about the temporal regularities in the world around us. We can use this knowledge to predict future events, guide our decisions, and plan the timing of our actions (Buhusi & Meck, 2005; Fraisse, 1984). Most visual scenes contain numerous sources of temporal information. In a scene containing multiple events, each event contains information about its own duration as well as information about the time between different events. As a result, the amount of temporal information available in our environment can become very large. Despite this abundance of temporal information, most temporal information is not relevant for our immediate behavior. This creates the need for effective selection of relevant temporal information, to avoid irrelevant information from affecting our behavior.

Visual attention provides a means by which relevant visual information can be selected against concurrent, irrelevant information (James, 1890). For example, directing attention towards one of multiple objects or features during adaptation leads to modulation of the resulting after-effects for these objects or features (Alais & Blake, 1999; Festman & Ahissar, 2004; Lankheet & Verstraten, 1995; Rhodes et al., 2011; Spivey & Spirn, 2000; Suzuki, 2001). These modulations of after-effect magnitude demonstrate differential processing as a result of attentional selection, and have been proposed to reflect changes in the strength of encoding of attended versus unattended information (Alais & Blake, 1999). This proposal is supported by neurophysiological studies demonstrating that attention modulates the response of visual neurons by increasing both response amplitude and selectivity (Desimone & Duncan, 1995; Moran & Desimone, 1985; S. O. Murray & Wojciulik, 2004; Reynolds et al., 1999; Treue & Martínez Trujillo, 1999). Together, these results suggest that visual attention provides a mechanism for the selective encoding of relevant versus non-relevant stimulus information by modulating the degree to which visual information is encoded.

While the role of attention in the selection of non-temporal properties is well established, there has been little investigation into its role in the selection of temporal properties. Several studies have demonstrated that the extent to which an event is attended can influence the perceived duration of that event (Block et al., 2010; Mattes & Ulrich, 1998; Tse et al., 2004). However, these studies do not address the role of attention in situations where multiple sources of duration information are present. This is surprising, as several theories of duration encoding have stressed the role of attention in gating duration information for subsequent encoding (Gibbon et al., 1984; Meck, 1984; Pariyadath & Eagleman, 2007; van Rijn et al., 2014; Zakay & Block, 1997). In the current study, we investigated the role of attention in the selective encoding of duration. We presented participants with multiple duration signals and investigated whether attending one source of duration information modulated duration encoding. We used duration-adaptation (Heron et al., 2012) to probe duration encoding and measured whether allocating attention towards one of multiple sources of duration information modulated the resulting duration after-effect (DAE). The DAE is a repulsive after-effect in which adaptation to a specific duration in one modality leads to a repulsive shift in the perceived duration of post-adaptation stimuli presented in the same modality (Heron et al., 2012; Li, Yuan, & Huang, 2015; Maarseveen, Hogendoorn, Verstraten, & Paffen, 2017; Shima et al., 2016). For example, adaptation to an 800 ms visual stimulus will lead to subsequent presentations of a visual stimulus with a shorter duration (i.e. 400 ms) to be perceived as even shorter, and presentations of a visual stimulus with a longer duration (i.e. 1200 ms) as even longer. This after-effect of adapting to duration is interpreted to reflect selective adaptation of duration-tuned channels as a result of the repeated encoding of their preferred duration (Heron et al., 2012). In line with this interpretation, modulation of the DAE is taken to reflect changes in the strength of encoding of the presented duration information.

In Experiment 1, participants adapted to two asynchronous streams of stimuli, each consisting of repetitions of a single duration stimulus that lasted either 200 or 800 ms (Figure 1). To probe the modulatory effect of attention, participants were instructed to detect duration oddballs in either the 200 or the 800 ms stream. Following adaptation, we measured the resulting DAE using a duration judgment task, in which participants compared the duration of an auditory reference (400 ms) to that of a visual test stimulus. We predicted that if attention modulates duration encoding, adaptation to the attended duration should increase relative to the adaptation to the unattended duration. In other words, attending the 800 ms durations should lead to a 400 ms test stimulus being perceived as shorter, compared to attending the

200 ms durations (implying stronger encoding of the attended duration). In a second experiment, we aimed to quantify the contribution of attended versus unattended durations to the DAE. To this end, we utilized adaptation to a reference duration – which predicts no DAE – to establish a baseline against which to measure the contribution of the attended and unattended durations. By doing so, we were able to probe the extent to which attended and unattended duration are encoded for further processing.

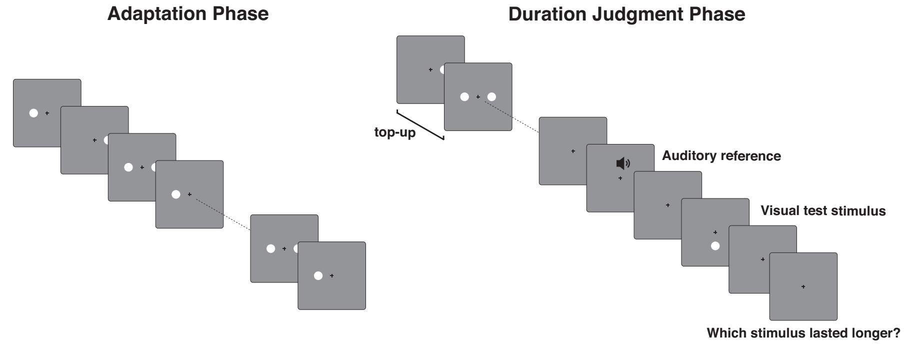


Figure 1. A schematic depiction of the experimental procedure. Adaptation Phase (left): Participants adapted to two asynchronous streams of duration stimuli presented left and right of fixation. Each stream consisted of repetitions of a single duration (i.e. 200 ms on the left, 800 ms on the right). In each stream ~10% of presentations consisted of duration oddballs with a shorter or longer duration. The participants' task was to maintain fixation and detect duration oddballs on one side (left or right) for the full duration of the adaptation phase. Duration Judgment Phase (right): Participants completed a duration judgment task in which they compared the duration of an auditory reference to that of a visual test stimulus. To maintain adaptation, a short top-up oddball detection phase preceded the duration judgment.

Results

Experiment 1

To examine the modulatory effect of attention on the DAE, we calculated the average Point of Subjective Equality (PSE) for when participants were attending either the 200 ms stream (A200) or the 800 ms stream (A800). Average PSEs for each attention condition can be found in Figure 2. We found clear evidence for attentional modulation of the DAE: attending a stream of 200 ms stimuli lead to a longer perceived duration of subsequent test stimuli ($M_{PSE} = 449.5$, SD = 108.3) compared to attending a stream of 800 ms stimuli ($M_{PSE} = 548.9$, SD = 124.1; Bayesian t-test: $BF_{10} = 205.34$). The Bayes factor (BF) reported here indicates that the current data were 205.34 times more likely to occur under the alternative hypothesis that attention modulated the DAE then under the null hypothesis that no attentional modulation occurred.

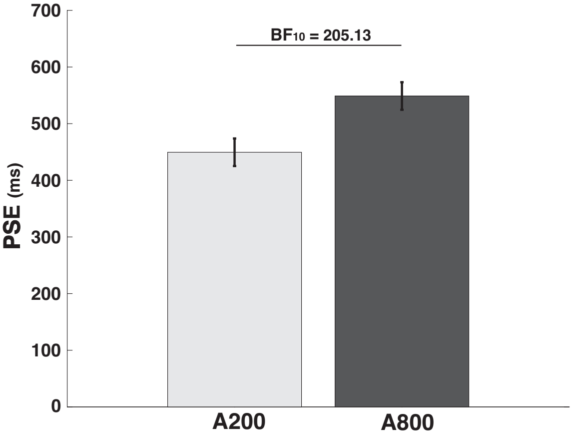


Figure 2. Average Point of Subjective Equality (PSE) for the cross-modal duration judgments following adaptation. Larger PSE values reflect shorter perceived duration for the test stimuli. Error bars reflect within-subject standard error (Cousineau, 2005; Morey, 2008). Bayes factors were used to describe the evidence for the alternative hypothesis that attention modulates the DAE. $BF_{10} > 3.0$ are considered evidence for the H_a (Jeffreys, 1998; Lee & Wagenmakers, 2013).

This result demonstrates that attention allows for the selective encoding of duration information. This finding that attention modulates the DAE is in line with effects of attentional selection on adaptation for non-temporal feature information (Alais & Blake, 1999; Lankheet & Verstraten, 1995; Rhodes et al., 2011; Suzuki, 2001). Interestingly, the magnitude of attentional modulation is similar in magnitude to the after-effects obtained by studies using adaptation to only a single stream of durations (Maarseveen et al., 2017). This suggests that the modulatory strength of attention is relatively large and that unattended durations might not contribute to the measured DAE. In other words, the magnitude of attentional modulation found here could reflect an absence of the encoding of the unattended durations. This possibility was evaluated in Experiment 2.

Experiment 2

In Experiment 2, we compared the contribution of attended and unattended durations to the measured DAE. Participants performed the oddball detection task under three conditions: repetitions of blobs lasting 200 and 400 ms, while performing the oddball task on the 200 ms blobs (A200|U400) or the 400 ms blobs (A400|U200), or to repetitions of blobs that both lasted 400 ms, while performing the oddball task on one of the 400 ms streams (A400|U400). By using adaptation to the baseline duration (400 ms) – which does not predict a DAE – we could examine the contribution of the attended (A200|U400 vs. A400|U400) and the unattended (A400|U200 vs. A400|U400) durations to the measured DAE.

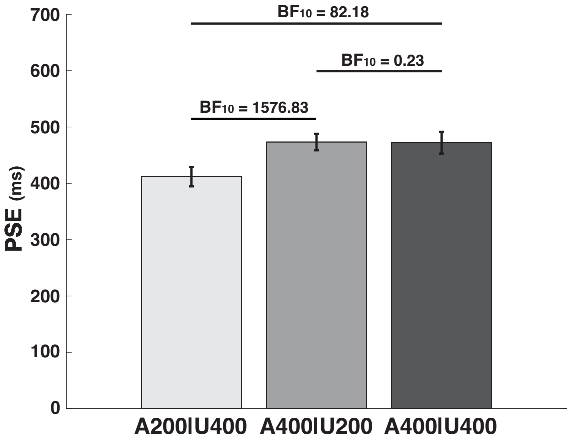


Figure 3. Average Point of Subjective Equality (PSE) for the cross-modal duration judgments following adaptation. Larger PSE values reflect shorter perceived duration for the test stimuli. Error bars reflect within-subject standard error (Cousineau, 2005; Morey, 2008). Bayes factors (BF_{10}) were used to describe the relative evidence for H_a vs. H_0. BF_{10} larger than 3.0 are considered evidence for the H_a, while BF_{10} smaller than 1/3 is considered evidence for the H_0 (Jeffreys, 1998; Lee & Wagenmakers, 2013).

As in Experiment 1, the data showed that attention modulated the magnitude of the DAE (Figure 3). A Bayesian within-subject ANOVA revealed evidence for the inclusion of the factor Attention (BF_{10} = 1689.81) in explaining the collected data. To further interpret this result, we conducted separate Bayesian t-tests for each pairwise comparison between the different attention conditions. This analysis showed that participants perceived the test stimuli as having a longer duration in the A200|U400 condition (M = 411.9 SD = 107.6) compared to the A400|U200 (M = 473.3, SD 106.1; BF_{10} = 1576.83) and the A400|U400 conditions (M = 472.1 SD = 120.8; BF_{10} = 82.18) (Figure 3). These findings corroborate our result from Experiment 1, demonstrating that attention can lead to relative shifts in the encoding of attended versus unattended durations. More importantly, we found evidence that there was no difference in the DAE between the A400|U200 and the A400|U400 conditions (BF_{10} = 0.233: data 4.29 times more likely under H_0). These results show that the DAE results from adaptation to the attended durations, with no evidence of a contribution of the unattended durations.

Discussion

In this study, we investigated whether attention gates the encoding of duration. We adapted participants to streams of differing durations and measured whether attending one of those streams modulated the DAE. The results provide strong evidence for attentional modulation of the DAE: test stimuli were perceived as having a longer duration when a stream of shorter durations was attended, compared to when a stream of longer durations was attended. We also investigated the degree to which attended and unattended durations are encoded by probing the contribution of attended and unattended durations to the DAE. We used adaptation to the reference duration (400 ms) – which predicts no DAE – to establish a baseline. We then used this baseline to compare adaptation to a non- reference duration when it was attended (A200|U400 vs. A400|U400) versus when it was not (A400|U200 vs. A400|U400). We found that the attended duration contributed to the DAE while the unattended duration did not. Given that the DAE is thought to result from repeated encoding of duration information, the lack of contribution of unattended durations to the DAE suggests that little to no encoding of the unattended duration occurred.

Earlier work on duration processing has demonstrated that manipulating the extent to which a stimulus is attended can influence the perceived duration of that stimulus (Block et al., 2010; Brown, 1995; Brown & West, 1990; Mattes & Ulrich, 1998; Tse et al., 2004). For example, increasing the attentional load during tasks involving duration leads to a decrease in the perceived duration of stimuli (Block et al., 2010). Furthermore, shifting spatial attention when encoding the duration of an event can lead to a decrease in its perceived duration (Cicchini & Morrone, 2009). In line with these findings, several theories of duration processing have included an attentional switch component as part of their model, which can lead to a decrease or increase in perceived duration depending on the state of the switch (Gibbon et al., 1984; Zakay & Block, 1997). This switch is often postulated to be a gating mechanism for duration signals, where changes in attention will change the amount of temporal information that is accumulated during an interval. While these studies provide evidence for a link between attention and perceived duration, they focus on manipulating the extent to which a single, task-relevant stimulus is attended. As such, these studies do not provide insight into the selective encoding of a relevant duration that is embedded in a scene with multiple sources of duration information. Our findings clearly demonstrate that attention does not only change the encoding of a single duration, but also plays a crucial role in selecting which of multiple source of duration information are encoded for further processing.

The current study shows that attention allows for the selective encoding of duration information. Given the role of attention in the selective encoding of duration, it is likely that attentional limits dictate the extent to which multiple durations can be effectively selected. In line with this idea, several studies have reported behavioral detriments when processing multiple, temporally overlapping durations (Ayhan, Revina, Bruno, & Johnston, 2012; Cheng et al., 2014; Morgan, Giora, & Solomon, 2008; van Rijn & Taatgen, 2008). Together with the current results, these findings point towards attentional limits in the encoding of duration, suggesting that duration processing is an effortful process with a limited capacity. Interestingly, capacity limits have been suggested to be related to the amount of overlap between the onsets and offsets of stimuli (van Rijn & Taatgen, 2008). This suggests that attention for the entire interval might not be needed and that attending the on- and offset of an interval could be sufficient to encode its duration. It would be interesting to further explore this relation and investigate whether selectively attending the onsets and offsets of stimuli is sufficient to allow for the selective encoding of duration.

The extent to which attention can modulate responses to a certain feature have been shown to reflect complexity of the feature and its position in the visual processing hierarchy (Suzuki, 2001). Several studies have shown that the magnitude of attentional modulation of after-effects increases as a function of the complexity of the encoded feature (Alais & Blake, 1999; Festman & Ahissar, 2004; Gibson, 1937; Lankheet & Verstraten, 1995; Rhodes et al., 2011; Spivey & Spirn, 2000; Suzuki, 2001, 2003). Furthermore, neurophysiological studies have demonstrated that attentional modulation of single cells responses to multiple stimuli increases as a function of the cells position in the visual processing hierarchy (Chelazzi, Duncan, Miller, & Desimone, 1998; Moran & Desimone, 1985; Reynolds & Chelazzi, 2004; Reynolds et al., 1999; Suzuki, 2001). For example, the contribution of unattended features to a cells response have been reported to vary from ~30% in early visual area V2, to nearly 0% in cells in IT (Chelazzi et al., 1998; Reynolds et al., 1999). Since we found that the DAE reflected the attended duration and not the unattended duration (a 100% relative contribution of attended durations), our results support the notion that duration is a complex feature encoded by mechanisms located at higher-level areas of the processing hierarchy. This conclusion is in line with recent studies demonstrating low spatial selectivity of the duration after-effect (Fulcher, McGraw, Roach, Whitaker, & Heron, 2016; Maarseveen et al., 2017). This finding indicate that duration-selective neurons possess relatively large receptive fields, again suggesting a locus in higher-level areas of the processing hierarchy (Maarseveen et al., 2017).

In the current paradigm we manipulated attention by having participants focus their attention towards a specific location in space and processing duration information at that location. This design confounds attention towards a spatial location and attention towards the feature 'duration'. As a result, it is not possible to conclude which of these types of attention is crucial for the attentional modulation observed in our experiments. A recent study investigating temporal recalibration found that attention towards the temporal order of events strongly modulated the resulting temporal recalibration compared to only attending the location at which the information is presented (Heron, Roach, Whitaker, & Hanson, 2010). This result demonstrates that attention towards temporal features can be crucial for adaptive temporal processing; underscoring the possibility that the modulation observed here might rely on directing attention towards the feature 'duration'. Future studies should aim to isolate specific types of attention to further understand its differential effects on temporal processing.

In our experiments we individually determined the duration of the auditory reference duration for each participant in an effort to create a reference duration that was perceptually equal to a 400 ms visual stimulus (a PSE of 400 ms). However, we observed an overall decrease in the perceived duration of the test stimulus in both Experiments (PSEs higher then 400 ms in all conditions), suggesting that the addition of the adaptation sequence influenced participants' perception of our auditory/visual stimuli in an unexpected way. This is most clearly visible in Experiment 2 in the A4000|U400 condition, where no DAE is predicted but the average PSE was 472.1 ms (~18% compression). One possible explanation for this compression of perceived duration is that the shifts in spatial attention from the adaptation location and the test location caused compression of the test interval. Attentional shifts during (or close to) an interval have been shown to compress the perceived duration of that same interval (Cicchini & Morrone, 2009). Given the long delays between the offset of the final adapter (top-up) and the subsequent onset of the test stimulus (ISI - auditory reference stimulus - ISI), we did expect compression to occur in our design. However, since we do not know when during the delay participant shifted their attention, we cannot exclude that such duration compression effects occurred. Alternatively, it is possible that other visual adaptation after-effects confounded our measurement of the DAE. A recent study demonstrated localized duration compression following adaptation to the non-temporal features (i.e. orientation) of visual stimuli (Cheng et al., 2014). While we designed our experiments to reduce adaptation to non-temporal features by introducing spatial separation of adaptation and test stimuli, it is possible that some adaptation to non-temporal features occurred. This would lead to overall compression of duration at the test location, and could explain the overall duration compression we observed here. In our current experimental design it is not possible to demarcate the different possible source of the overall duration compression present in our results. Regardless of its origin, duration compression seems to occur across all conditions independently of our manipulation. As such, the observed compression does not affect our predictions and conclusion regarding the attentional modulation of the DAE observed in both experiments. Additional work will be needed to understand duration compression in these adaptation designs and improve similar designs for future studies.

In this study, an adaptation paradigm was used to probe the encoding of duration by measuring the effect of repeated encoding (or a lack thereof) on subsequent behavior. Although we find no evidence for a contribution of unattended durations to the DAE, the indirect measure used here does not allow us to claim that no encoding of the unattended duration occurred per se. For one, participants were aware of the unattended stimulus being presented, indicating that some information about the unattended stimulus was encoded. However, given the lack of a contribution of the unattended durations to the DAE, encoding of the unattended duration was either too sparse or too weak to lead to a measurable DAE. In other words, while we do not argue for the absolute lack of a representation of the unattended duration per se, we do argue that any information encoded about the unattended stimulus will not lead to a robust, stable representation, and as such will not impact the perception and behavior of the observer.

Our results demonstrate that attention gates the encoding of duration: attended durations lead to a DAE, while unattended durations do not. These findings are in line with earlier work suggesting attentional limits on the processing of duration and support the idea that duration encoding is an effortful process that requires gating by visual attention. We conclude that visual attention underlies the selection of relevant temporal information when multiple sources are present.

Methods

Participants

Data were collected from 12 participants (2 male, age M = 28, SD = 8.41) in Experiment 1, and 20 participants (7 male, age M = 25.55, SD = 7.72) in Experiment 2. All participants had normal or corrected-to-normal vision, and did not suffer from any neurological disorders. All participants were informed of their rights and gave written informed consent before the experiment started. Both experiments were approved by the local ethics committee of the Faculty of Social and Behavioral Sciences of Utrecht University and conducted in accordance with the guidelines expressed in the Declaration of Helsinki.

Apparatus and stimuli

The same materials were used for both experiments. All visual stimuli were presented on a linearized Electron 22BlueIII CRT monitor (1280 x 1024, 100Hz), controlled by a Dell OptiPlex 7040 workstation (Windows 10) using Matlab 2015b. For Experiment 1, gaze position measurements were taken using the EYE TRIBE tracker, sampling at 30 Hz. This eye tracker was controlled using the PyGaze software package and eye tribe toolbox for Matlab (Dalmaijer, 2014; Dalmaijer et al., 2014). Furthermore, a chin- and headrest were used to increase head stability during tracking. Auditory stimuli consisted of a burst of white noise (60 dB, 0.01 ms ramp) presented through a Sennheiser on-ear headset.

For both experiments, all stimuli were presented on a gray background (9.6 cd/m^2), accompanied by a white central fixation dot (64.7 cd/m^2). Visual stimuli consisted of Gaussian blobs (40.8 cd/m^2, 62% peak Michelson contrast, $\sigma = 0.625°$) presented at 5.8° of visual angle from fixation (Figure 1). Adaptation stimuli were always presented left and right of fixation; test stimuli for the duration judgment task were presented below fixation. These distances and locations were selected so that participants could clearly distinguish each stream and the test stimuli. Additionally, we used this spatial setup to reduce adaptation to the non-temporal stimulus features of each stream (Zhou et al., 2014), while still assuring that adaptation to duration at both stream locations could be measured at the test location (Maarseveen et al., 2017).

Procedure

Participants adapted to duration by viewing two streams of Gaussian blobs displayed to the left and right of a central fixation cross. Each stream consisted of repetitions of a single duration (ISI of 500-750 ms), with incidental duration oddballs (either shorter or longer) being presented on 10% of trials. To manipulate attention, participants were instructed to fixate the center of the screen and perform a duration-oddball detection task on the stream left or right of fixation. Performance on the oddball detection task was kept at 75% correct throughout the experiment by varying the oddball durations using an Accelerated Stochastic Approximation (ASA) staircase (Kesten, 1958). In Experiment 1, blobs in one stream lasted 200 ms while the blobs in the other stream lasted 800 ms. As a result, participants adapted in two conditions; attending the 200 ms stream (A200) or the 800 ms stream (A800). In Experiment 2, participants performed the oddball detection task in three conditions: repetitions of blobs lasting 200 and 400 ms, while performing the oddball task on the 200 ms blobs (A200|U400), repetitions of blobs lasting 200 and 400 ms, while performing the oddball task on the 400 ms blobs (A400|U200), or to repetitions of blobs that both lasted 400 ms, while performing the oddball task on one of the 400 ms streams (A400|U400). Adaptation to 400 ms repetitions was used here because it predicts no DAE when testing with a 400 ms reference duration. As such, the A400|U400 condition provides an appropriate baseline that is similar in visual presentation and task demands to the other conditions, while not predicting any DAE.

For all adaptation presentations, the longest duration was presented 100 times, while the number of repetitions for the shorter durations was set so that the two streams were approximately equal in total duration. For example, in Experiment 1, the 800 ms stimulus was presented 100 times, while the 200 ms stimulus was presented ~173 times. This method assured that presentation of the two streams terminated at around the same time, keeping the chance that the last stimulus belonged to either stream at ~50%. The order in which each stream of different durations was presented left or right of fixation was counterbalanced and presented in random order for each participant.

Following adaptation, we measured the DAE using a cross-modal duration judgment task. Each duration judgment trial started with top-up presentations of the oddball detection task with the aim of maintaining adaptation throughout the test period. In all cases, 4 repetitions of the longest duration were presented with the number of shorter durations selected to match the total stream duration for the longest duration stream. Following the top-ups, participants compared the duration of an auditory reference to that of a visual test stimulus and indicated which of the two durations they perceived as having a longer duration. For each trial, the duration of the visual test stimulus was varied using a Minimum Expected Entropy Staircase (Saunders & Backus, 2006).

In the duration judgment task the auditory reference always preceded the visual test stimulus, which should result in a time order error, with a longer perceived duration for the reference stimulus compared to the test stimulus (Jamieson & Petrusic, 1975). To account for this error, we set the auditory reference duration to be perceptually equal to the 400 ms visual test stimulus for each individual participant at the start of the experiment. Participant completed a duration judgment task in which they compared a visual reference duration of 400 ms to that of an auditory test duration, the duration of which was varied using an ASA staircase (Kesten, 1958). Resulting estimates of the PSE were used to create the auditory reference used for the adaptation experiment. By doing so, we assured that the auditory reference duration in the adaptation experiment was perceived as being equal to the 400 ms (unadapted) visual test stimulus. The mean matched auditory reference durations for Experiment 1 and 2 were 362.37 ms (SD = 75.46) and 375.66 ms (SD = 102.90) respectively.

Each experimental session started with a practice block, in which participants practiced the duration judgments task (30 trials), followed by the auditory reference experiment (70 trials). Next, participants practiced the oddball detection task for each combination of attended durations and attended side. The aim of this practice session was to acquaint participants with the tasks and to derive initial discrimination thresholds, which were used to inform the adaptive staircase used to maintain detection performance at ~75% for the main experiment. For the main experiment, participants completed 4 blocks (50 trials each) in Experiment 1 and 6 blocks (30 trials each) in Experiment 2. This resulted in a total of 100 trials for each attention condition for Experiment 1 and 60 trials per attention condition in Experiment 2. The total sessions lasted ~3 hours for Experiment 1 and ~2 hours for Experiment 2.

Gaze control

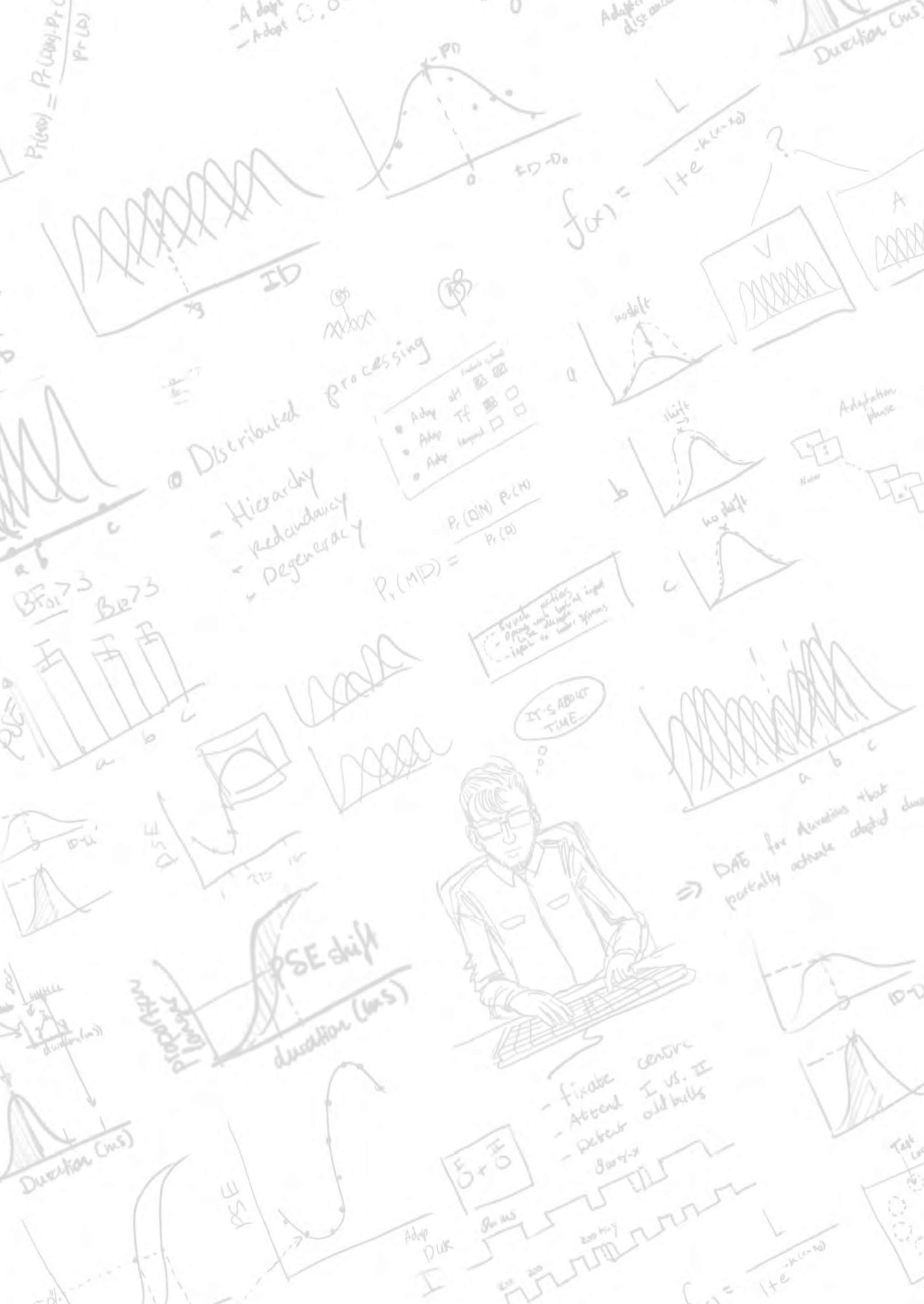
To assure that participants fixated the center of the screen and not the attended stimulus, gaze data was collected for 7 out of 12 participants. Gaze position was tracked during adaptation and during duration judgments. What is more, duration judgments were contingent on accurate fixation, with deviations from fixation larger than 2.5° of visual angle leading to termination of the trial. Terminated trials were recycled.

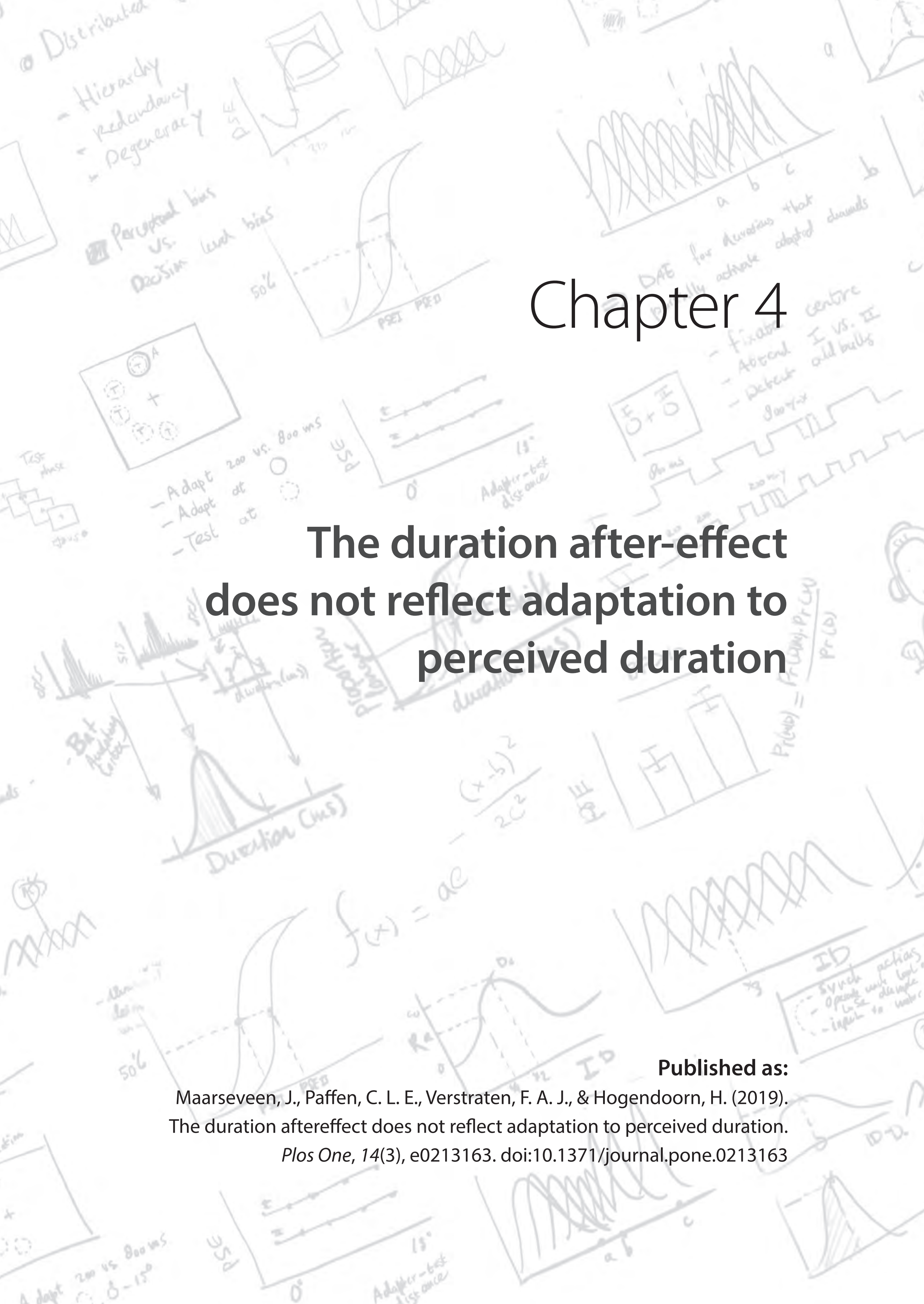
We analyzed all successfully collected samples for both the adaptation (M = 97.24%, SD = 3.11%) and top-up presentations (M = 95.92%, SD = 3.81%). Analysis of these data showed that participants fixated within an area of 2° of visual angle on 90.66% (SD = 4.44%) of all successfully gathered samples during adaptation, and 91.91% (SD = 2.17%) of the samples collected during top-ups. Furthermore, participants failed to maintain fixation on 7.33% (SD = 3.8%) of all duration judgment trials. Together these results indicate that participants had little trouble following the instruction to maintain fixation at the center of the screen.

Analysis

For both experiments we calculated the PSE for each of the attention conditions for each participant, by fitting a psychometric function using a logistic regression. These PSEs indicate the duration of the visual test stimulus that was perceived as being equal to the presented auditory reference. As such, higher PSEs indicate shorter perceived duration of the test stimulus and lower PSEs indicate longer perceived duration of the test stimulus. Average PSEs can be found in Figures 2 and 3 (see Supplementary materials S1 and S2 for individual data). The depicted error bars represent within-subject standard errors calculated using per-subject normalization of the data (Cousineau, 2005; Morey, 2008). These standard errors reflect within-subject variability making them more informative of the outcome of the analyses of the within-subject effects reported here. The analyses for both experiments were conducted using Bayesian analysis in JASP (JASP Team, 2017; Marsman & Wagenmakers, 2017). For all analyses a common uninformative prior (Cauchy prior with width .707) was used.

In Bayesian analysis 'significance' is expressed in terms of a Bayes factor which indicates relative evidence between competing models (e.g. the model describing H_0 vs. the model describing H_a). For example, a Bayes factor: $BF_{10} = 10$ indicates that the collected data is 10 times more likely to occur under the H_a compared to the H_0. Because the Bayesian framework allows for quantification of the evidence for both the H_a and H_0 – something that is not possible using traditional inferential statistics – we can evaluate evidence that results in two conditions are not different from one another (as is applied in Experiment 2). To evaluate the evidence for or against each hypothesis we used a common rule of thumb in which $BF_{10} > 3$ is taken as sufficient evidence in favor of H_a and $BF_{10} < 1/3$ as evidence in favor of H_0 (Jeffreys, 1998; Lee & Wagenmakers, 2014). Importantly, it should be noted that while larger or smaller Bayes factors can be directly interpreted as larger amounts of evidence for their respective hypotheses, it does not inform about the effect size associated with the observed difference. To allow for insight into the effect size all reports will include the mean and standard deviation of each condition, and we encourage readers to evaluate the results visually in the provided figures.


Distributed processing
- Hierarchy
- Redundancy
- Degeneracy
IT'S ABOUT TIME
PSE shift
duration (ms)
Proportion longer
Duration (ms)
no shift
shift
no shift
a
b
c
PSE
Adap DUR
- fixate centre
- Attend I vs. II
- Detect odd balls
=> DAE for durations that partially activate adapted
Adaptation phase
ID
PD
ID-D0
f(x) = L / 1+e^{-k(x-x0)}
Pr(M|D) = Pr(D|M) Pr(M) / Pr(D)
BF01 > 3
B10 > 3



Chapter 4

The duration after-effect does not reflect adaptation to perceived duration

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Abstract

Recent studies have provided evidence for a role of duration-tuned channels in the encoding of duration. Duration encoding in these channels is thought to reflect the time between responses to the onset and offset of an event. This notion is in apparent conflict with studies that demonstrate that the perceived duration of an event can vary independently from the time separating its perceived onset and offset. Instead, these studies suggest that duration encoding is sensitive to other temporal aspects of a sensory event. In the current study, we investigated whether duration-tuned channels encode duration based on the time between the on- and offset of an event (onset-offset duration), or if they encode a duration corresponding to the perceived duration of that event. We used a duration illusion to dissociate onset-offset duration and perceived duration and measured whether repeated exposure to illusion-inducing stimuli caused adaptation to the onset-offset duration or the perceived duration of these illusion-inducing stimuli. We report clear evidence for adaptation to the onset-offset duration of illusion-inducing stimuli. This finding supports the notion that duration-tuned mechanisms respond to the time between the onset and offset of an event, without necessarily reflecting the duration perceived, and eventually reported by the participant. Implications for the duration channel model and the mechanisms underlying duration illusions are discussed.

Introduction

Recently, it has been proposed that duration-tuned mechanisms underlie the encoding of duration (Heron et al., 2012; Ivry, 1996). According to this idea, the brain contains groups of duration-tuned neurons that respond selectively to specific ranges of durations. Summation of the population response of these groups of duration-tuned bandpass-neurons (or channels) allows for implicit temporal signals to be transformed into an explicit code for duration that is both accurate and reliable. This explicit signal can then be stored, manipulated, and used to guide subsequent behavior (Heron et al., 2012).

The proposal for channel-based encoding of duration is very similar to the mechanisms that are thought to underlie the encoding of a range of other sensory features such as orientation (Gibson, 1933; Hubel & Wiesel, 1959), motion direction (Albright, 1984; Anstis et al., 1998), pitch (Romani et al., 1982), and numerosity (Burr & Ross, 2008; Harvey et al., 2013). Similar to these other stimulus features, support for the channel-based encoding of duration comes from studies demonstrating duration tuning in both behavioral and neuronal responses (Hayashi et al., 2015; Heron et al., 2012). For example, several studies have shown that adaptation to duration leads to a duration after-effect (DAE) for subsequently presented durations (Heron et al., 2012, 2013; Li, Yuan, & Huang, 2015; Maarseveen et al., 2017; Maarseveen, Hogendoorn, Verstraten, & Paffen, 2018; Shima et al., 2016). More specifically, these studies demonstrate that adaptation to a particular duration in one modality causes the perceived duration of subsequent durations in that same modality to shift away from the adapted duration. For example, after adapting to a visual event lasting 400 ms, the perceived duration of visual events with a shorter duration (i.e. 200 ms) will decrease, while the perceived duration of events with a longer duration (i.e. 800 ms) will increase. These results are taken to reflect selective adaptation of duration-tuned neurons, resulting in a shifted population response for durations close to the adapted duration (Heron et al., 2012; Kohn, 2007). Similarly, studies have shown that training observers to discriminate durations leads to increased performance on the trained but not the untrained durations (Bueti & Buonomano, 2014). In line with the adaptation results, these results suggest channel-specific training benefits and are similar to the results observed for discrimination training in other features encoded in a channel-based fashion (Bueti & Buonomano, 2014; Schoups, Vogels, Qian, & Orban, 2001). Furthermore, a recent fMRI study using fMRI adaptation demonstrated a decreased BOLD-response in the (right) inferior parietal lobule (IPL) following repetitions of identical duration (Hayashi et al., 2015). This fMRI adaptation did not occur when the two durations were different, indicating that the BOLD-responses in this area reflected selective responses to specific durations.

These findings support the notion that selectively tuned channels underlie the encoding of duration in a way that is similar to the encoding of other sensory properties. However, it is not clear what aspect(s) of a sensory event these channels are responding to. According to one idea, duration channels are sensitive to the temporal distance separating the neural responses to the onset and offset of a sensory event. In other words, duration-tuned channels are thought to respond differentially to the offset of an event depending on the time since the response to the onset of that same event (Heron et al., 2012). Evidence for these onset-dependent offset responses comes from animal physiology studies demonstrating duration-tuned responses in single cells in both Brown bat auditory cortex (Ehrlich et al., 1997; Wu & Jen, 2008), cat auditory cortex (He et al., 1997) and cat visual cortex (Duysens et al., 1996).

However, this idea of encoding duration based on the temporal distance between the onset and offset responses is in apparent contrast with the fact that the perceived duration of an event can be manipulated, without any concurrent changes in our perception of the onset and offset of that same event (Johnston et al., 2006; Kaneko & Murakami, 2009). For example, in the Temporal Frequency Induced Time Dilation (TFITD) illusion, increasing the speed or temporal frequency of an event increases its perceived duration without affecting the perceived onset and offset of that same event (Kaneko & Murakami, 2009). Assuming that the duration encoded by the duration channels informs our perception of duration, we would expect a strong relation between the temporal distance separating the perceived moments of onset and offset, and the duration perceived by the observer. As such, this dissociation between the separation of perceived onset and offset on the one hand, and perceived duration on the other, seems in contrast with the idea that duration channels extract duration based solely on the temporal distance between onsets and offsets of the sensory signal.

To address this contrast, we used duration adaptation to probe the duration-tuned channels and adapted observers to a TFITD-inducing stimulus. By doing so, it is possible to dissociate between adaptation to the temporal distance separating the onset and offset of the sensory signal (onset-offset duration) and adaptation to a duration corresponding to the duration perceived by the observer. Participants adapted to repetitions of one of three stimuli: a rotating radial grating (the illusion-inducing stimulus); to a static radial grating matched to the temporal distance between the onset and offset of the illusion-inducing stimulus (the onset-offset matched stimulus); or to a static radial grating matched to the perceived duration of the illusion-inducing stimulus (the perceptually matched stimulus). Next, we measured whether the resulting DAE for the illusion-inducing stimulus reflected adaptation to either its onset-offset duration or its perceived duration. If participants adapt to the onset-offset duration of the illusion-inducing stimulus, the resulting DAE should match the DAE following adaptation to the onset-offset matched stimulus. However, if participants adapt to the perceived duration of an event, the DAE for the illusion-inducing stimulus should match the DAE for the perceptually matched stimulus.

Methods

Participants

25 Observers participated in this experiment. Of these 25, 5 participants were excluded after an initial measurement because they did not display a sufficiently large TFITD illusion (time dilation < 33%). Excluded participants completed an unrelated experiment. Details about the exclusion procedure can be found in the 'TFITD illusion magnitude estimation' section under Procedure. The remaining 20 participants completed the experiment (10 male, $M_{age} = 24.30$, $SD = 4.73$). All participants were naïve as to the purpose of the experiment and had normal or corrected-to-normal vision. Written informed consent was obtained before the experiment began. Following participation, participants received course credits or monetary compensation. This study was approved by the Ethics Committee at the Faculty of Social and Behavioral Sciences of Utrecht University and was conducted in accordance with the Declaration of Helsinki.

Materials & Stimuli

All stimuli were presented on a linearized 22-inch CRT monitor (1024 x 768 pixels, 100 Hz refresh rate) controlled by an Apple Mac Mini. Stimulus presentation was controlled using MATLAB 2015b (MathWorks, Inc.) and the Psychophysics

Toolbox (Brainard, 1997; Pelli, 1997). Participants viewed the stimuli with their head resting in a chinrest placed 57 cm from the screen. The auditory stimuli were presented using a Sennheiser HD201 on-ear headset. All stimulus timings were verified using a dual-channel oscilloscope.

All stimuli consisted of a circular radial grating (diameter of 2.0°) with a sinusoidal luminance modulation (100% Michelson contrast) of 4 cycles. On each presentation, this stimulus was either static or rotating at 2.08 cycles/second. This resulted in each individual point of the stimulus being modulated sinusoidally at 8.33 Hz. All stimuli were presented on a gray background (32.5 cd/m²) and accompanied by a central fixation cross (64.3 cd/m²). Each radial grating was presented peripherally at a distance of 4° degrees from the central fixation cross. In all tasks, test and reference stimuli were presented at one of four possible positions, the location of which was counterbalanced across participants (0, 90, 180, or 270° angle from fixation). All adaptation stimuli were presented randomly across 10 possible locations at a 45 to 315° angle from the test stimulus with an inter stimulus interval (ISI) ranging between 500 -750 ms. This spatial configuration was used to reduce the overall adaptation to the non-temporal stimulus features and the temporal frequency of our adaptation stimuli. In addition, this configuration resulted in a minimum separation of 3.06° of visual angle between the adaptation and test stimuli. At this distance any adaptation to the non-temporal features or temporal frequency of the adaptation stimuli should not affect our measurement of perceived duration at the test location (Johnston et al., 2006; Zhou et al., 2014), while still allowing for effective measurement of the DAE (Maarseveen et al., 2017). Auditory reference stimuli consisted of a burst of white noise (60dB) with a 10 ms linear onset and offset ramp.

Procedure

TFITD illusion magnitude estimation. Since each participant differs in the magnitude of his or her TFITD illusion, the duration of the perceptually matched stimuli and the central reference stimulus needs to be tailored to each individual participant. We estimated the magnitude of the TFITD illusion for individual participants by having them completed a visual duration judgment task. In this task, participants compared the duration of a reference grating that lasted 300 ms. to a static test grating with a variable duration. Depending on the condition, the reference grating was either static or rotating. The order in which the reference and test were presented was randomized and counterbalanced across trials. For all presentations, we used an ISI jittered between 500-750 ms. The point of subjective equality (PSE) for each condition (static, rotating) was acquired over the course of 80 trials by varying the duration of the test stimulus using an accelerated stochastic approximation (ASA; Kesten, 1958) set to converge to the 50% correct point. The ASA staircase aims to effectively converge on a selected response probability by quickly reducing step size. As a result, relatively few trials are required to produce a reliable estimate of the selected threshold. After participants completed this task, we used the PSEs estimated by each staircase to calculate an illusion factor (PSE_{static} / $PSE_{rotating}$). We then multiplied this factor by the duration of the onset-offset matched stimulus (300 ms), to acquire the duration of the perceptually matched stimulus for the individual participant (M = 572.60 ms, SD = 129.00).

The current design relies on comparing a single critical condition (adaptation to illusion-inducing stimuli) to two 'baseline' conditions (adaptation to onset-offset matched stimuli & perceptually matched stimuli). As such, it is necessary to be able to dissociate between adaptation to the onset-offset matched baseline and the perceptually matched baseline. In other words, our design requires an observable difference in the PSEs following adaptation to the onset-offset matched and perceptually matched stimuli. The magnitude of the DAE depends strongly on the temporal distance between the adaption durations and the reference duration (Heron et al., 2012). However, in the current study the temporal distance between adaptation durations and the reference durations is contingent on the magnitude of each individuals TFITD illusion. As such, it is problematic when participants do not display a significant TFITD illusion, as they do not provide data that contributes to answering our research question. To address this issue, we set an inclusion criterion at a minimum illusion magnitude of 33.33% (100 ms). By using this criterium, we aimed to optimize the inclusion of participants, while still obtaining a measurable DAE between our two 'baseline' conditions (onset-offset matched, perceptually matched). Participants who did not meet the inclusion criterion were excluded from the experiment and completed an unrelated experiment instead. As, mentioned above, five participants who had signed up were excluded based on this criterion. The remaining 20 participants completed the main adaptation experiment.

Next, we set the individual reference duration by calculating the logarithmic midpoint between the durations of the onset-offset matched

(300 ms) and perceptually matched stimuli (M = 572.60 ms). This logarithmic midpoint (M = 412.09 ms, SD = 45.43) was used as the visual reference duration against which the DAE for each of the adaptation conditions was measured. Earlier work suggests that duration-selective mechanisms show logarithmic scaling in preferred duration and sensitivity (Duysens et al., 1996; He et al., 1997; Heron et al., 2012; Yumoto et al., 2011). By using the logarithmic midpoint, we assure equal (perceptual) distance from the reference duration to the adaptation durations in the onset-offset matched and perceptually matched stimulus conditions. This procedure is similar to those used in earlier experiments, and allows us to measure the DAE as opposite shifts in perceived duration using the same range of test stimuli (Heron et al., 2013; Maarseveen et al., 2017, 2018).

Auditory reference calibration. Our experiment employed a cross-modal duration judgment task in which the auditory reference duration always preceded the visual test stimulus. This procedure typically leads to a time order error (Jamieson & Petrusic, 1975) where, on average, the auditory reference will be perceived as having a longer duration than its visual counterpart with the same duration. To account for this, we set the duration of the auditory reference stimulus individually for each participant so that the perceived duration of the auditory stimulus was perceptually equivalent to that individual's visual reference duration. To acquire each individual auditory reference duration, participants completed a cross modal duration judgment task in which they compared the duration of a static reference grating to the duration of an auditory test stimulus. For each individual participant, the duration for the static reference grating was based on the individual reference duration calculated in the previous task. The duration of the auditory test stimulus was varied using an ASA staircase set to converge at the 50% correct point over the course of 60 trials. The resulting estimates of the Point of Subjective Equality (PSE) were used to set the duration of the auditory reference used in the adaptation experiment (M = 370.63 ms, SD = 149.75).

Adaptation experiment. In separate blocks, participants adapted to 100 repetitions of one of three stimuli: 1) The illusion-inducing stimulus, which consisted of a rotating radial grating that lasted 300 ms. 2) The onset-offset matched stimulus, which consisted of a static radial grating that was matched to the onset-offset duration of the illusion-inducing stimulus (300 ms). 3) The perceptually matched stimulus, which consisted of a static radial grating matched to the perceived duration of the illusion-inducing stimulus. The duration of the perceptually matched stimulus was set individually for each participant (M = 572.60 ms). During adaptation, participants did not perform any task and were instructed to maintain fixation on the central fixation cross.

Each adaptation phase was followed by a test phase in which participants completed a cross-modal duration judgment task. Each duration judgment started with 4 top-up repetitions of the adaptation stimulus, followed by the auditory reference and a static visual test stimulus (ISI = 500 - 750 ms). The participant's task was to indicate which of the reference - test pair had a longer duration (Figure 1). The duration of the test stimulus was varied using a Minimum Expected Entropy Staircase (MEES; Saunders & Backus, 2006). This staircase allows for effective estimation of the PSE while still varying the duration of the stimuli presented to the participants. This variance in the duration of the test stimulus helps assure that participants pay attention to the task. In each block, participants completed 30 trials. In total, participants completed 9 blocks accounting to a total of 270 trials. This corresponded with participants completing a total of 90 trials per staircase, one for each adaptation condition. The entire experiment lasted about 2 hours and included a 15-minute break.

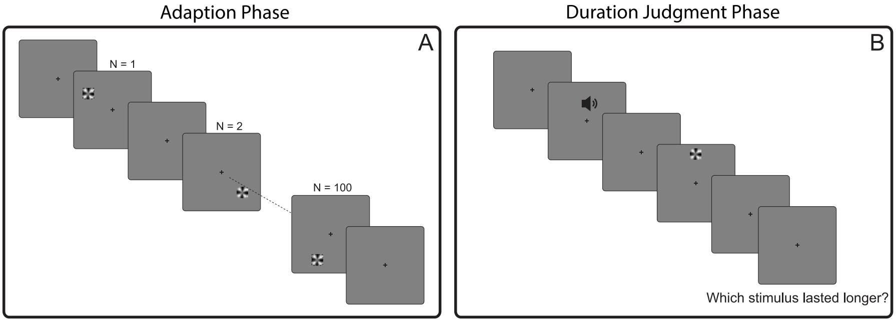


Figure 1. An overview of the experimental procedure for the adaptation experiment. Adaptation Phase (A): participants adapted to 100 repetitions of one of three adaptation stimuli: an illusion-inducing rotating radial grating (300 ms, 8.33Hz), a static radial grating matched to the onset-offset duration of the illusion-inducing stimulus (300 ms, static), or a static grating matched to the perceived duration of the illusion-inducing stimulus ($M_{duration}$ = 572.60, static). Duration Judgment Phase (B): participants completed a duration judgment task in which they compared the duration of an auditory reference to that of a static visual test stimulus.

Analysis

We calculated the PSE for each of the three adaptation conditions for each participant, by fitting a psychometric function using a logistic regression. The resulting PSEs correspond to the duration of the visual test stimulus that was perceived as being equal to the auditory reference duration. As such, higher PSEs indicate lower perceived durations of the test stimuli, while lower PSEs indicate higher perceived durations of the test stimuli.

All data were analyzed using Bayesian analysis using the open source statistics program JASP (Marsman & Wagenmakers, 2017). For all analyses, a common uninformative prior (Cauchy prior with width .707) was used. In Bayesian analysis a Bayes factor (BF) is used to express the relative probability that the current data were collected under one hypothesis (i.e. H_a) vs. the probability that the data were collected under another hypothesis (i.e. H_0). This relative evidence provided by the Bayes factor can then be evaluated using a common rule under which a $BF_{10} > 3$ is taken as evidence in favor of H_a and $BF_{10} < 1/3$ as evidence in favor of H_0 (Jeffreys, 1998; Lee & Wagenmakers, 2013). It is important to note here that while higher/lower BFs indicate higher relative evidence for one model over another, it does not indicate a larger effect size. To judge the size of each effect, we encourage the reader to evaluate the provided figure as well as the averages and standard deviations reported for each statistical test.

One of the advantages of a Bayesian approach is that it allows to quantify the evidence for both our H_a's (the results from two conditions are different), as well as for our H_0's (the results from two conditions do not differ). This advantage over inferential statistics is critical in our current design. Our main hypothesis resolves around the notion that the DAE following adaptation to illusion inducing stimuli will reflect either adaptation to the onset-offset duration of the perceptually matched duration of that stimulus. In other words, we expect that the DAE following adaptation to illusion inducing stimuli will not differ from the DAE found in either the onset-offset matched or perceptually matched stimulus conditions. Quantification of evidence for the H_0 allows us to test this hypothesis appropriately.

Results

Average PSEs for each of the adaptation conditions can be found in Figure 2. The depicted error bars represent within-subject standard errors calculated using per-subject normalization of the data (Cousineau, 2005; Morey, 2008). Error bars depicting the standard of the mean illustrate both the between-subject and within-subject variance in a dataset. These depictions describe the total variance in the data and can help indicated the variability across subjects. However, in a design focused on within-subject differences, error-bars depicting the standard error of the mean have little informational value about the outcome of the within-subject analyses (Cousineau, 2005). The within-subject standard errors used here reflect only the within-subject variability making them more predictive of the outcome of the analyses of the within-subject effects that were reported here.

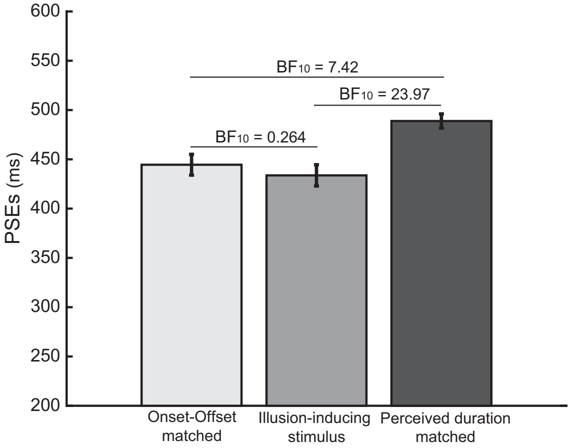


Figure 2. Average PSEs for each of the three Adaptation conditions. Average PSEs for when participants adapted to the onset-offset matched stimulus (300 ms, static), the illusion-inducing stimulus (300 ms, 8.33Hz), and the perceptually matched stimulus (M = 572.60 ms, static). BFs are given for all Bayesian paired sample t-tests with $BF_{10} > 3$ indicating evidence that the PSEs are different and $BF_{10} < 1/3$ indicating evidence that they are not. Error bars reflect confidence intervals based on the within-subject variability of the data (Cousineau, 2005; Morey, 2008).

The PSE data were analyzed using a Bayesian repeated measures ANOVA with PSE as a dependent measure and Adaptation Type (onset-offset matched stimulus, illusion-inducing stimulus, perceptually matched stimulus) as a factor. This analysis revealed a main effect of Adaptation type ($BF_{10} = 8.14$). To gain insight into this main effect we conducted three subsequent pairwise comparisons (Bayesian paired samples t-test) comparing each combination of the adaptation conditions.

First, we compared PSEs between the onset-offset matched stimulus and the perceptually matched stimulus. We found that adaptation to the onset-offset matched duration lead to a longer perceived duration of the test stimulus (M = 444.51 ms, SD = 133.11) compared to adaptation to the perceptually matched duration (M = 488.86 ms, SD = 149.90; BF_{10} = 7.42). In other words, adapting to a static stimulus which lasted 300 ms (onset-offset matched stimulus) caused subsequent test durations to be perceived as having a longer duration, compared to adaptation to a static stimulus with a longer duration (M = 572.60 ms; perceptually matched stimulus). This finding replicates the DAE observed in earlier studies and demonstrates that our method can be used to dissociate adaptation to the durations of the onset-offset matched and perceived duration matched stimuli.

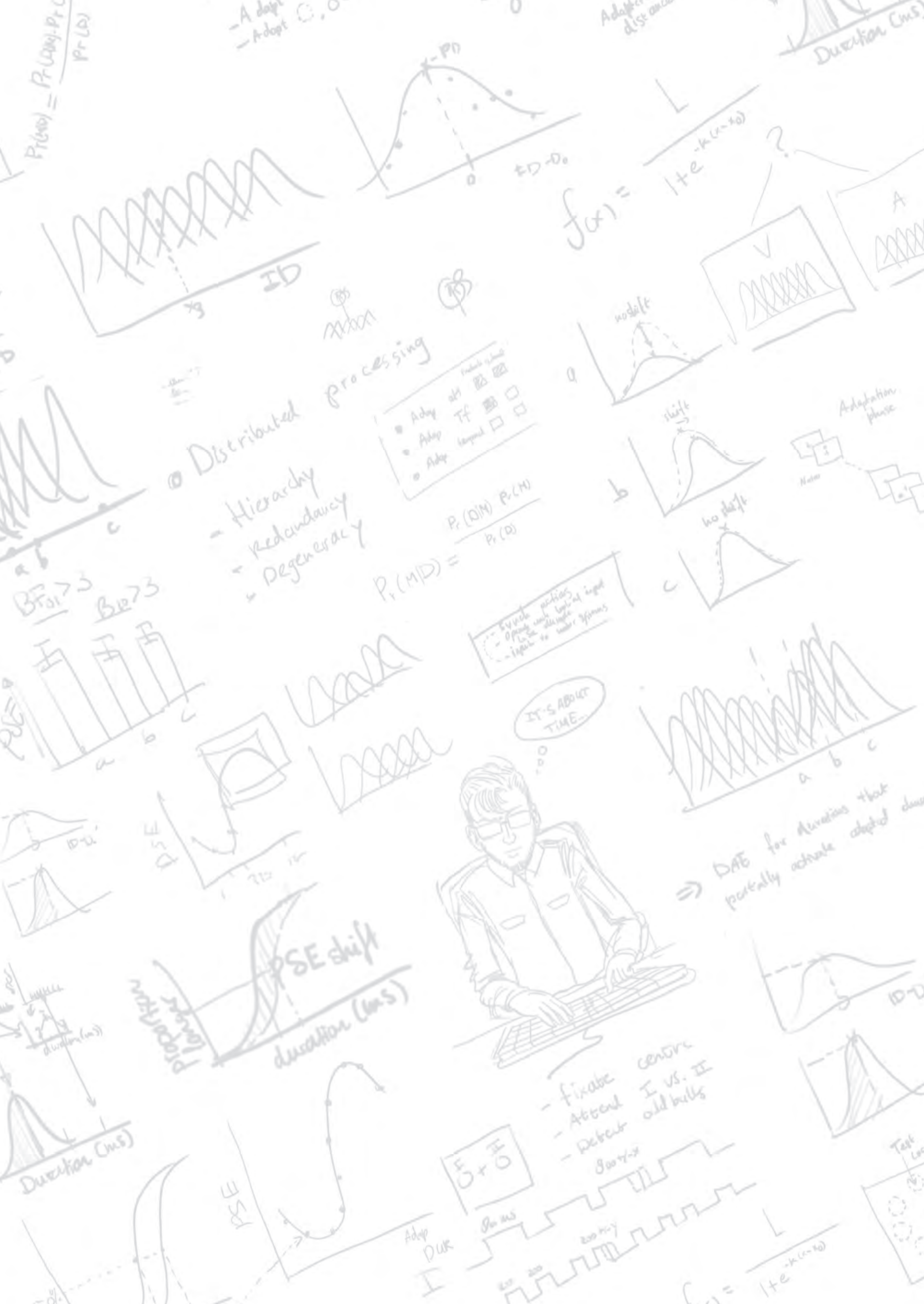
Next, we compared the DAE following adaptation to the illusion-inducing stimulus (M = 433.72 ms, SD = 160.70) to each of the matched conditions and found that the resulting DAE differed from the DAE for the perceptually matched duration (BF_{10} = 23.97), but not from the DAE for the onset-offset matched duration (BF_{10} = 0.264). This suggests that participants adapted to the onset-offset duration of the illusion-inducing stimulus instead of to a duration corresponding to the perceived duration of the illusion-inducing stimulus.

Discussion

In this study we addressed the apparent contradiction between the proposal that duration-tuned channels encode duration based on the time between the responses to the onset and offset of an event, and the fact that our perception of duration can be dissociated from this onset-offset duration of an event. To this end, we adapted participants to an illusion-inducing stimulus that is known to cause shifts in the perceived duration of an event, without affecting its perceived onset and offset (Kaneko & Murakami, 2009). Participants adapted to one of three types of stimuli: an illusion-inducing rotating radial grating, a static grating matched to the onset-offset duration of the illusion-inducing stimulus, and a static grating matched to the perceived duration of the illusion-inducing stimulus. We measured the resulting DAE and found that the DAE for illusion-inducing stimuli did not differ from the DAE for the onset-offset matched stimuli but did differ from the DAE for the perceptually matched stimuli. In other words, participants adapted to the *onset-offset duration*, and not to a duration corresponding to the *perceived duration* of the illusion-inducing stimulus. This result supports the proposal that duration channels are sensitive to the temporal distance between the onset and offset responses that result from a sensory event; possibly via neurons that show onset-dependent offset responses (Heron et al., 2012). We conclude that channel-based duration encoding is based on the temporal distance between the onset and offset of an event and does not necessarily corresponds to the perceived duration of that same event.

Our results demonstrate that duration-tuned mechanisms are sensitive to the temporal distance between the onset and offset responses that result from the sensory event that is being encoded. As a result, the duration encoded by these mechanisms does not necessarily correspond to the duration eventually perceived by the observer. This suggest that channel-based encoding reflects an initial processing step, the output of which is then further transformed during subsequent processing. This idea is consistent with a more hierarchical view of duration encoding in which duration information is accumulated from multiple sources across multiple stages of processing (van Wassenhove, 2009). In line with this idea, Heron and colleagues (2013) demonstrated that the channel-based encoding of duration occurs before the integration of duration information from the different senses. In addition, several studies have demonstrated that duration perception depends on a wide range of factors that reflect different stages of cognitive processing. For example, studies on memory and memory mixing have demonstrated that memory about other magnitudes can influence estimations of duration (Cai & Wang, 2014; Rammsayer & Verner, 2015). Furthermore, studies focusing on the role of contextual experience have demonstrated that duration estimates can be influenced by both the sensory and response history of previous duration estimates (Jazayeri & Shadlen, 2010; Roach, McGraw, Whitaker, & Heron, 2017). In addition to these behavioral findings, a large number of cortical and subcortical areas have been implicated in the processing of duration information (see for example: Hayashi et al., 2015; Jantzen, Steinberg, & Kelso, 2005; Meck et al., 2008; Mello et al., 2015; Merchant, Pérez, et al., 2013; Spencer & Ivry, 2013). Together, these studies support the notion that duration processing occurs in multiple stages throughout the brain in a distributed and possibly task-specific manner.

Our findings that duration channels do not adapt to a duration corresponding to the perceived duration of our TFITD inducing stimuli draws into question the mechanisms underlying this illusion. Duration illusions are often assumed to reflect direct changes in the encoding of duration (i.e. changing the clock speed), and as such have often been used to study the mechanisms underlying the initial encoding of duration information from sensory information (Droit-Volet & Wearden, 2002; Eagleman, 2008; Kanai et al., 2006; Pariyadath & Eagleman, 2007; Xuan, Zhang, He, & Chen, 2007). In particular, TFITD has been proposed to reflect changes in the rate at which temporal information is accumulated during duration encoding (Kanai et al., 2006). In contrast with this assumption, our results suggest that TFITD occurs after the initial (channel-based) encoding of duration and likely reflects modulation of subsequent processing steps. In a more general sense, our finding calls into question the extent to which other duration illusions reflect direct changes in the (rate of) encoding of duration information. That being said, it is important to underscore that only a single illusion was tested in the current study. Since it is likely that different duration illusions influence duration processing in a distinct manner (i.e. at different stages of processing) we should be careful in generalizing the results reported here. In fact, some duration illusions have been reported to be caused by changes in the response to the onset and/or offset of events (Kanai & Watanabe, 2006). Under the current model, these illusions *would* predict changes in the response of the duration-tuned channels and corresponding changes in the duration perceived by the observer. Since most duration illusions are smaller in magnitude then the TFITD illusion employed here, it could prove difficult to apply our paradigm to other duration illusions. Hopefully, future experiments will give insight in the relation between duration-tuned responses and the wide range of duration illusions already reported in the literature.


Distributed processing
- Hierarchy
- Redundancy
- Degeneracy
IT'S ABOUT TIME
PSE shift
duration (ms)
Proportion longer
PSE
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no shift
- fixate centre
- Attend I vs. II
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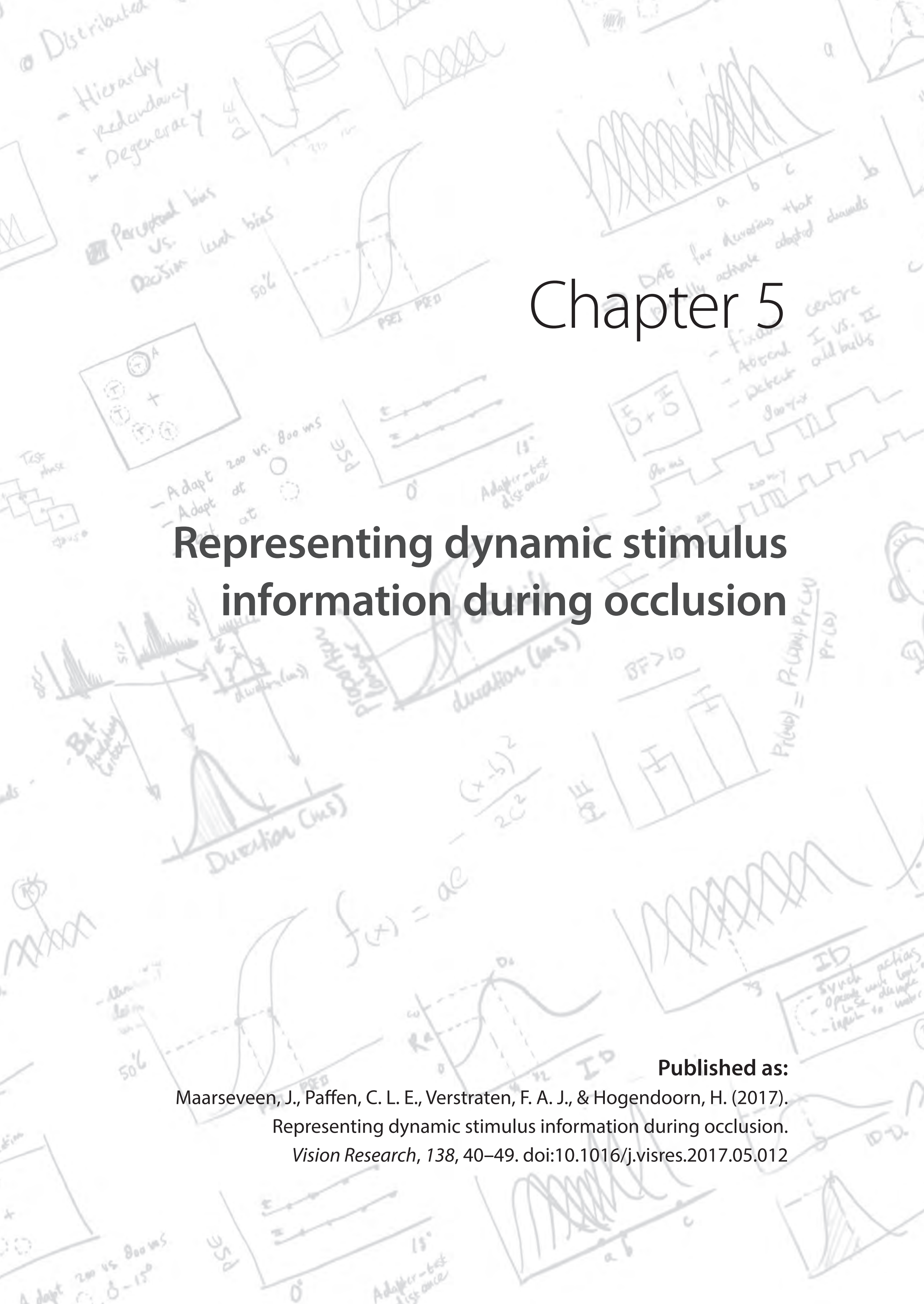

Chapter 5

Representing dynamic stimulus information during occlusion

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Abstract

Human observers maintain a representation of the visual features of objects when they become occluded. This representation facilitates the interpretation of occluded events and allows us to quickly identify objects upon reappearing. Here we investigated whether visual features that change over time are also represented during occlusion. To answer this question we used an illusion from the time perception domain in which the perceived duration of an event increases as its temporal frequency content increases. In the first experiment we demonstrate temporal frequency induced modulation of duration both when the object remains visible as well as when it becomes temporarily occluded. Additionally, we demonstrate that time dilation for temporarily occluded objects cannot be explained by modulations of duration as a result of pre- and post-occlusion presentation of the object. In a second experiment, we corroborate this finding by demonstrating that modulation of the perceived duration of occluded events depends on the expected temporal frequency content of the object during occlusion. Together these results demonstrate that the dynamic properties of an object are represented during occlusion. We conclude that the representations of occluded objects contain a wide range of features derived from the period when the object was still visible, including information about both the static and dynamic properties of the object.

Introduction

During daily life, objects constantly move in and out of sight, temporarily depriving us of direct visual information about these objects. However, even though retinal input is disrupted we tend to experience these objects as persisting in space and time (Michotte, 1950). Several studies have shown that both animals and human observers behave as if the occluded object is still present (e.g. Baillargeon, 1986; Churchland, Chou, & Lisberger, 2003; Von Hofsten, Kochukhova, & Rosander, 2007; Van Wermeskerken et al., 2011). This suggests that we maintain an internal representation of an object while it is occluded. This representation of occluded objects has been a topic of interest in several fields investigating situations of both partial and full occlusion. Behavioral studies investigating amodal completion – the process of filling in occluded parts of an object – have shown that both the shape (Rensink & Enns, 1998) and color (Dadam, Albertazzi, Canal, & Micciolo, 2012; Pinna, 2008) are completed for the occluded segment of the object. This representation of the occluded segment is formed automatically (M. M. Murray et al., 2006) and can influence both the interpretation of concurrent events (Joseph & Nakayama, 1999; Sekuler & Palmer, 1992) as well as subsequent behavior (Gerbino & Salmaso, 1987). Similarly, studies on full occlusion show that information about object shape, color, velocity, and motion direction can be maintained across periods of occlusion (Flombaum et al., 2009; Hollingworth & Franconeri, 2009; Moore, Stephens, & Hein, 2010; Saiki, 2003). This information can be used to track and identify objects across episodes of occlusion (Hollingworth & Franconeri, 2009; Scholl & Pylyshyn, 1999; von Hofsten et al., 2007), as well as predict events occurring during occlusion (Baillargeon, 1986; Benguigui, Ripoll, & Broderick, 2003; von Hofsten et al., 2007). Furthermore, it has been shown that an object under occlusion can be the target of object-based attention, suggesting that the representation contains information about feature binding that occurred before occlusion (Behrmann, Zemel, & Mozer, 1998; Moore, Yantis, & Vaughan, 1998). On a neural level, the representation of occluded objects resembles that of visible, non-occluded objects. Several studies have reported a wide network of activity in visual areas of the brain that overlaps with activity found when objects are not occluded. This network includes both visual areas involved in the processing of higher order stimulus information such as object shape (Kourtzi & Kanwisher, 2001; Kovács et al., 1995), object identity (Hulme

& Zeki, 2007), and relative location (Graziano, Hu, & Gross, 1997), as well as retinotopically mapped areas involved in the processing of basic features of the visual scene (Ban et al., 2013; Rauschenberger, Liu, Slotnick, & Yantis, 2006).

Together, these studies suggest that the representation of occluded objects incorporates a wide range of features, derived from the period that the object was still visible. These features are represented by visual areas of the brain that also represent these features during perception of the visible object (Ban et al., 2013). Furthermore, these representations seem to be object-like in nature (Behrmann et al., 1998) enabling us to understand events that occur during occlusion as well as to categorize objects on reappearance (Baillargeon, 1986; Scholl & Pylyshyn, 1999).

Most studies on occlusion have focused on the static visual properties of an object (e.g. color or shape). However, in many natural situations image properties such as shape, luminance, and location change over time. For example, when a tennis ball temporarily disappears behind a wall, its location continues to change during occlusion. Additionally, if the ball is spinning, its visual features also change along its trajectory. Representing these feature changes and the rate at which they occur could aid in the interpretation of events occurring during occlusion as well as facilitate the identification of objects upon reappearing. For example, a change in velocity or spin would suggest that the object interacted with another object while under occlusion. Up until now, only the change of location over time (motion) has been studied (Ban et al., 2013; Olson, Gatenby, Leung, Skudlarski, & Gore, 2004; von Hofsten et al., 2007). These studies have shown that both location and speed are represented during occlusion. For example, (Olson et al., 2004) reported that activity in human MT/V5 for occluded motion was similar to that observed during visible motion, suggesting that area MT/V5 continues to represent the velocity and direction of the object during its occlusion. In addition, a study by (Ban et al., 2013) showed that the retinotopic representation of the position of an occluded object in areas V1 and V2 is updated over the course of the occlusion period. This suggests that the temporal derivative of position – velocity – is used to extrapolate the predicted position of the object during occlusion. It is unknown however, whether dynamic changes other than motion, such as those occurring for the spinning ball, also continue to be represented during occlusion.

Here we present two experiments in which we investigate whether dynamic changes in the visual features of an object are represented during occlusion. To this end, we investigated whether the temporal frequency content of a luminance-modulated (i.e. flickering) object is represented during occlusion. We used a well-known temporal illusion – temporal frequency induced time dilation – in which the perceived duration of an event increases as a result of an increase in its temporal frequency content (Kanai et al., 2006; Ortega & López, 2008). By combining this property of duration perception with a situation in which the object becomes occluded, we can investigate whether the dynamic properties of an object are represented during occlusion. We hypothesized that if the temporal frequency content of an occluded object is represented during occlusion, it should lead to patterns of time dilation similar to those observed during normal, visible presentation.

Experiment 1

We presented participants with a duration reproduction task in which participants replicated the duration of a stimulus that was either static or luminance-modulated at different temporal frequencies. On each trial the stimulus was paired with the presentation of an occluder that moved either in front or behind the stimulus, and then returned to its starting position after a short delay. As a result the stimulus either remained visible or became temporarily occluded. If the temporal frequency content of the stimulus is represented during occlusion we should observe longer reproduction for higher temporal frequency modulations, both for the non-occluded and occluded stimuli.

To assure that participants are aware of the onset, offset, and temporal frequency content of the stimulus, a brief pre- and post- occlusion presentation of the stimulus is needed. These presentations could lead to time dilation, making it difficult to interpret any time dilation found for occluded stimuli. To solve this issue, we added a control condition in which the stimulus remained visible, but the luminance-modulation was faded out and back in over the period in which the occlusion event occurred. This extinction condition simulates the pre- and post- occlusion presentation of temporal frequency content in the occluded condition, without presentation of the deletion (and accretion) cues that would lead to maintenance of the temporal frequency content of the stimulus. As such any effect of initial presentation should occur for non-occluded, occluded and extinction stimuli. On the other hand, any effect of the representation of temporal frequency during occlusion should only be observed for occluded stimuli and not for stimuli with fading luminance-modulation.

To summarize, if temporal frequency is represented during occlusion we should observe time dilation both when the stimulus remains visible as well as when it becomes occluded. Additionally, time dilation for the occluded stimuli should be larger than any time dilation observed in the extinction condition.

Material and Methods

Participants. A total of 20 healthy adults participated in this study (7 male; mean age=22.5, SD=3.41). All participants had normal or corrected-to-normal vision and normal stereoscopic vision. They received monetary reward or course credits as compensation for their participation and were naïve as to the purpose of the experiment. The experiment was conducted in line with the principles expressed in the Declaration of Helsinki and received approval by the local ethics committee. All participants were informed that they could stop their participation at any time and that the data would be processed anonymously. After agreeing with these terms all participants signed a written informed consent form.

Apparatus and stimuli. Stimuli were presented on two linearized 24-inch LCD monitors (screen resolution at 1920 x 1080 pixels, 60 Hz refresh rate) controlled by single Windows workstation (Windows 10) running MATLAB 2010A (MathWorks, Inc.) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Both screens were viewed dichoptically through a mirror setup. Throughout the experiment images from the right screen were projected to the right eye and images from the left screen to the left eye. The total distance between the participant and each of the screens was ~85 cm. From this distance the full screen subtended 35.38° x 20.08° of visual angle. Head movements were restrained using a chinrest.

All stimuli were presented on both monitors and were presented on a grey background (62.5 cd/m^2). To facilitate binocular fusion between the two images all presentation was accompanied by a square, pink-noise frame (96.79% Michelson contrast) that started 11.2° x 11.4° from the center of the screen and subtended 2.8° x 2.8° of visual angle.

Procedure. Each trial started with a white central fixation cross (322 cd/m^2; 0.57° x 0.57°) and a grey-black textured occluder (4.1° x 2.28°; black: 0.33 cd/m^2, grey: 30.3 cd/m^2) presented 2.85° above the fixation cross (Figure 1). The perceived depth of the occluder relative to the frame was manipulated by creating disparity between the occluder on the left and right screen (+/-0.12°), causing the occluder to be perceived as either in front or behind the frame. To facilitate binocular fusion and the perception of depth, vertical edges were added to the occluder in the form of a smaller grey rectangle, starting at 2.6° x 0.78° from the center of the occluder location and subtending 1.50° x 1.50°. After 250ms the fixation cross was replaced with a test stimulus consisting of a white circle (diameter: 1.9°) that was either static (214 cd/m^2) or luminance-modulated at a temporal frequency of 5 or 10 Hz. Luminance modulation was sinusoidal with a peak contrast of 50.12% (Michelson contrast). After a short delay from the onset of the test stimulus (33, 67, 100 ms) the occluder started to move downwards with a speed of 13.68°/s until its center aligned with the center of the screen after 217ms. Depending on the condition, this resulted in the occluder moving either in front (Occluded condition) or behind (Non-Occluded & Extinction conditions) of the stimulus, in line with the depth cue derived from the occluder location relative to the frame. The occluder then maintained its position for 466–533ms, 766–833ms, or 1066–1133ms depending on the duration of the test stimulus. Following this period, the occluder moved up to its original position (at 13.68°/s) and remained on the screen. In the Extinction condition the amplitude of the luminance modulation of the test stimulus faded out and back in with a linear profile. The goal of this fading was to mimic the disappearance of the temporal frequency content in the Occlusion condition. The decrease in amplitude started when the occluder first touched the stimulus, 67 ms after motion onset, and ended when the stimulus and occluder completely overlapped 200ms after motion onset. Similarly, the luminance modulation was reintroduced over a period of 133 ms starting with the reappearance of the stimulus. The participants' task was to reproduce the duration of the test stimulus by pressing and holding down the right-arrow key. After reproduction the next trial was initiated by pressing spacebar.

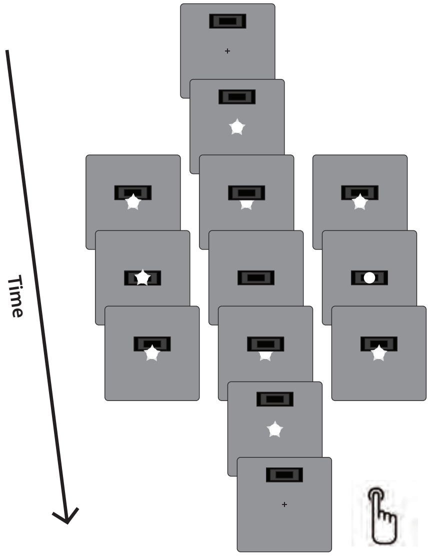


Figure 1. Overview of the procedure. Participants reproduced the duration of a test stimulus by pressing and holding a key. The test stimuli were presented in three different occlusion conditions (Non-Occluded, Occluded, and Extinction: shown from left to right). Depending on the condition, the occluder either moved behind the test stimulus (Non-Occluded and Extinction) or in front of the test stimulus (Occlusion). In the Extinction condition, luminance modulation faded in and out across the period when stimulus and occluder overlapped.

Participants were tested in a 3 x 3 x 3 within-subject factorial design. The three factors were Duration (1000, 1300, or 1600ms), Occlusion (Non-Occluded, Occluded, Extinction), and Temporal Frequency (Static, 5 Hz, or 10 Hz luminance modulation). Participants completed two blocks consisting of either a combination of Non-Occluded and Occluded trials or a combination of Non-Occluded and Extinction trials. Blocked presentation assures that occluded presentations are assumed to reflect an occluded presentation of the Non-Occluded trials – were the temporal frequency modulation persists – and not an occluded presentation of the Extinction trials. The order of the two types of blocks was counter-balanced across conditions. For each block, all combinations of factors were counterbalanced and assigned randomly across trials. Within each block every combination of factors was repeated 30 times, resulting in a total of 540 trials per block and a grand total of 1080 trials across the entire experiment. During each block participants were given three self-timed breaks spread evenly across the experiment. Both experimental blocks lasted about 45-min and were separated by a 15-min break.

Results

For each participant and each unique combination of conditions, individual trials with responses more than two standard deviations away from the mean were removed from further analysis. This resulted in the removal of a total of 902 trials (4.18%). We then calculated the average reproduced duration for each condition for each participant (see Figure 2). The resulting data were analyzed using a 3 x 3 x 3 repeated measures ANOVA, with Reproduction Duration as the dependent measure and Duration (1000, 1300, 1600ms), Temporal Frequency (Static, 5Hz, and 10Hz), and Occlusion (Non-Occluded, Occluded, Extinction) as factors. For all results Greenhouse-Geisser corrections were used if Mauchly's test of sphericity showed that the assumption of sphericity was violated. For all post-hoc comparisons using t-tests reported in the manuscript, p-values were adjusted for multiple comparisons using the Holm-Bonferroni correction method (Holm, 1979). The corrected p-values are reported for ease of interpretation, alpha is at 0.05 for all statistical tests. The error bars in all images reflect within-subject standard errors, calculated using per-subject normalization of the data (Cousineau, 2005; Morey, 2008).

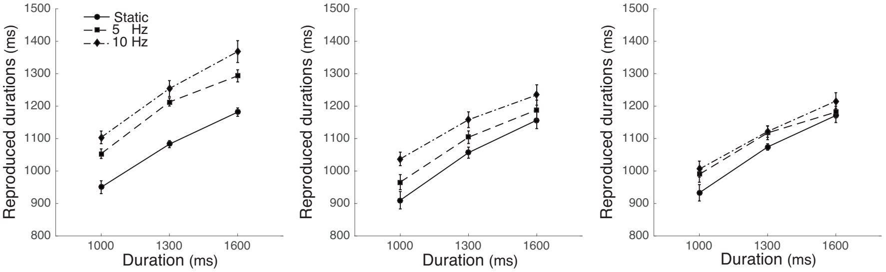


Figure 2. Average Reproductions plotted as a function of the presented durations for each Temporal Frequency. Separate plots for each of the Occlusion conditions, left to right: Non-Occluded, Occluded, Extinction. Error bars reflect within-subject standard errors.

We observed a main effect of Duration ($F(1.04,19.73) = 57.42$, $p < 0.001$, $\eta^2 = 0.751$). Pairwise comparisons revealed that this effect was due to an increase in reproduction durations over the three measured test durations ($p < 0.001$ for all comparisons) indicating that participants' responses were sensitive to the presented duration. We also observed a main effect of Temporal Frequency, $F(1.22,23.24) = 36.06$, $p < 0.001$, $\eta^2 = 0.66$. Subsequent paired sample t-tests for the main effect of Temporal Frequency revealed that participants reproduced shorter durations in the Static condition compared to both the 5 Hz (*t*(19) = -5.07, $p = 0.007$) and 10 Hz conditions (*t*(19) = -8.44, $p = 0.007$). Additionally, reproductions in the 5 Hz condition were shorter than those in the 10 Hz condition (*t*(19) = -3.37, $p = 0.007$). Additionally, we observed a main effect for Occlusion (*F*(1.46,27.73) = 7.14, $p = 0.006$, $\eta^2 = 0.27$). Subsequent paired sample t-tests revealed that this effect was characterized by significantly longer reproductions in the Non-Occluded condition compared to both the Occlusion and Extinction conditions (*t*(19) = 3.27, $p = 0.007$ and *t*(19) = 3.28, $p = 0.007$, respectively). There was no significant difference between the Occlusion and Extinction conditions (*t*(19) = 0.01, p = 0.995). Finally, we observed a significant interaction between Duration and Temporal Frequency (*F*(2.51,47.66) = 10.42, $p < 0.001$, $\eta^2 = 0.35$). There were no other significant interactions: Duration*Temporal Frequency (*F*(2.85,54.01) = 1.87, $p = 0.148$, $\eta^2 = 0.09$), Duration*Occlusion (*F*(2.57,48.81) = 1.35, $p = 0.271$, $\eta^2 = 0.07$), and Duration * Temporal Frequency * Occlusion (*F*(8,152) = 1.84, $p = 0.074$, $\eta^2 = 0.09$).

To understand the observed interaction between Temporal Frequency and Occlusion we compared the magnitude of time dilation between each of the Occlusion conditions. By doing so we can assess whether, and how, the observed time dilation differed between each of the occlusion conditions. We expected a larger effect of temporal frequency content in the Non-Occluded condition compared to both the Occlusion and the Extinction conditions. More importantly, if information about the temporal frequency content of the test stimulus is maintained during occlusion we expect the observed time dilation to be larger for the Occluded condition compared to the Extinction condition. Because there was no significant interaction that included the factor Duration we first averaged our data across the different test durations. We then subtracted the average reproductions for the Static condition from the average reproductions for both the 5 Hz and 10 Hz conditions for each of the occlusion conditions. The resulting difference scores reflect the amount of time dilation occurring in the 5 Hz and 10 Hz conditions for each of the occlusion conditions (Figure 3).

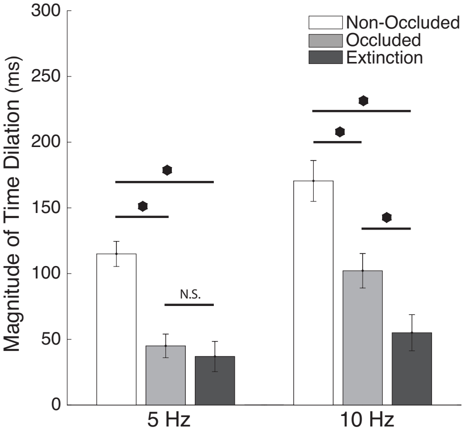


Figure 3. Magnitude of Time dilation, plotted separately for each Temporal Frequency (5Hz, 10Hz), for each of the Occlusion conditions (Non-Occluded, Occluded, Extinction). Diamonds indicate significant deviation tested at an alpha of 0.05 (corrected for multiple comparisons). Error bars reflect within-subject standard errors.

Next we conducted a 2 x 3 repeated-measures ANOVA with Magnitude of Time Dilation as the dependent variable and Temporal Frequency (5 Hz, 10 Hz) and Occlusion (Non-Occluded, Occlusion, Extinction) as factors. This analysis revealed a main effect of Temporal Frequency ($F(1,19) = 18.47$, $p < 0.001$, $\eta^2 = 0.49$), indicating that there was more time dilation in the 10Hz condition compared to the 5Hz condition. Next, we observed a main effect of Occlusion ($F(2,38) = 12.21$, $p < 0.001$, $\eta^2 = 0.39$), which shows that the amount of time dilation was different between the three Occlusion conditions. We analyzed this difference by conducting pairwise comparisons, revealing that the amount of time dilation was significantly higher in the Non-Occluded condition, compared to both the Occluded ($t(19) = 3.61$, $p = 0.004$) and Extinction conditions ($t(19) = 4.38$, $p = 0.001$). No significant difference was observed between the Occluded and Extinction conditions ($t(19) = 1.45$, $p = 0.16$). However, we did observe a significant interaction effect between Temporal Frequency and Occlusion condition ($F(2,38) = 5.22$, $p = 0.01$, $\eta^2 = 0.22$). This significant interaction seemed to reflect a larger difference between the different occlusion presentations in the 10 Hz condition compared to the 5 Hz condition (Figure 3). To investigate this apparent difference in the magnitude of time dilation in the 5Hz and 10Hz conditions, we conducted two separate repeated-measures ANOVAs with Magnitude of Time Dilation as the dependent variable and Occlusion (Non-Occluded, Occluded, Extinction) as a factor. For the 5 Hz condition we found a main effect of Occlusion (*F*(2,19) = 12.09, $p < 0.001$, $\eta^2 = 0.39$). Subsequent paired sample t-tests revealed that this effect reflected a significant difference between the Non-Occluded and Occlusion and Extinction conditions, *t*(19) = 4.81, $p < 0.001$ and *t*(19) = 4.07, $p < 0.001$ respectively. There was no significant difference between the Occlusion and Extinction conditions (*t*(19) = 0.44, $p = 0.665$). For the 10 Hz condition we again found a main effect of Occlusion (*F*(2,19) = 11.19, $p < 0.001$, $\eta^2 = 0.37$). Subsequent paired sample t-tests revealed that this effect reflected a significant difference between the Non-Occluded and the Occlusion and Extinction conditions, *t*(19) = 2.70, $p < 0.028$ and *t*(19) = 4.40, $p < 0.001$ respectively. More importantly, there was a significant difference between the Occlusion and Extinction conditions (*t*(19) = 2.15, $p = 0.044$), with more time dilation during occlusion presentations compared to the extinction presentations.

Discussion

We found that the presentation of luminance-modulated stimuli (5, 10 Hz) led to longer reproductions compared to static stimuli and that this effect was larger for the high temporal frequency stimuli (10 Hz) compared to the lower temporal frequency stimuli (5 Hz). In other words, the participants judged the duration of the stimulus as being longer with increased temporal frequency content. This replicates the results of earlier studies in which increases in temporal frequency content cause dilation of perceived duration (Kanai et al., 2006; Ortega & López, 2008). Subsequent analysis showed that significant time dilation occurred in each of the three occlusion conditions (Non-Occluded, Occluded, Extinction). More importantly, we compared the magnitude of time dilation between each of the Occlusion conditions. We found significantly larger time dilation for non-occluded presentations compared to the occluded and extinction presentations, for both the 5Hz and 10Hz presentations. Crucial to answering our question, we observed larger time dilation in the Occluded condition compared to the Extinction condition, but only for the 10Hz luminance-modulated stimuli. In the 5 Hz condition, no significant difference between Occlusion and Extinction conditions was observed. These results show that the observed time dilation for the occluded presentations did not results from the pre- and post- occlusion presentation of the stimulus and instead reflected the continued representation of temporal frequency content during periods of occlusion.

Experiment 2

Experiment 1 provides the first evidence for the representation of dynamic features during occlusion. In this experiment, we used the Extinction condition as a control for any time dilation that resulted from the pre- and post- occlusion presentation of the modulated stimulus. This Extinction condition was constructed to mimic the decrease in temporal frequency content that occurs during occlusion, without the deletion and accretion cues that accompany occlusion. As a result, the way in which the temporal frequency content is erased differs between the two conditions. In the Occluded condition the temporal frequency content of the stimulus is removed as the edge of the occluder moves over the stimulus. In the Extinction condition however, this loss of temporal frequency content occurs gradually across the entire stimulus. This difference in the way in which the stimulus loses its temporal frequency content might result in a difference between the points in time at which the stimulus is perceived as losing its temporal frequency content. Furthermore, differences in the temporal frequency and contrast profiles of stimuli have been shown to cause changes in the perceived duration of an event (Bruno, Ayhan, & Johnston, 2012, 2015; Bruno & Johnston, 2010; Matthews, 2011). While the modulations used in these studies do not match the conditions presented here, they underscore the sensitivity of duration perception to differences in low-level visual properties. As a result, we cannot be sure that differences in the way by which temporal frequency content was erased in both conditions contribute to the differences we found in the reproduced durations.

To address this concern, we designed a second experiment in which we compared two occlusion events that were visually identical but differed in the expected temporal frequency content of the stimulus during occlusion. Earlier work on object permanence and inhibition of return (IOR) has shown that manipulating expectations about occluded stimuli can lead to changes in preferential looking behavior (Spelke, Kestenbaum, Simons, & Wein, 1995) and IOR (Jefferies, Wright, & Lollo, 2005). These studies demonstrate that expectations can change observers' representations of occluded objects. By manipulating participants' expectations about the temporal frequency content of stimuli during occlusion, we can probe the representation of temporal frequency without changing the visual properties of the presentations.

Similar to experiment 1 we presented participants with a duration reproduction task in which they reproduced the duration of stimuli that either remained visible or became occluded after a short delay. We manipulated participants' expectations about the temporal frequency content of the stimulus during occlusion by changing the context in which the occlusion event occurred. Each block of trials contained a single type of stimulus: a static stimulus (Static), a stimulus modulated at 10 Hz (Continuous), or a stimulus whose 10Hz modulation was temporarily extinguished (Disrupted). The goal of this blocked design was to support the expectation that the occluded stimulus had the same properties as the non-occluded stimulus presented in the same block. As a result participants should have different expectations for the properties of the stimulus while it is under occlusion. For the Continuous modulation blocks, the continuously modulated stimulus for the non-occluded trials will provide evidence that the stimulus continues to flicker while disappearing behind the occluder. In the Disrupted modulation blocks, however, the non-occluded trials will provide evidence that the stimulus will cease to flicker once it is occluded. To strengthen this expectation of the stimulus' properties during occluded, we added induction trials at the start of each block in which the occluder moved in front of the stimulus but was semi-transparent. This allowed participants to observe the stimulus while it was being 'occluded', strengthening the assumption of a common fate for non-occluded and occluded stimuli.

Crucially, the disruption of the temporal frequency modulation always occurred after the occluder had fully moved in front or behind the stimulus. As a result, the occlusion event for the continuous and disrupted stimuli is visually identical, differing only in the expected temporal frequency of the stimulus during the occlusion event. We hypothesized that if temporal frequency is represented during occlusion, we should find more time dilation for occlusion events presented in the context of continued modulation, compared to those presented in the context of disrupted modulation.

Methods

Participants. 21 Healthy participants completed this experiment (7 male; mean age=23.24, SD=3.63). All participants had normal or corrected-to-normal vision and normal stereoscopic vision. All participants gave written informed consent before participating and received monetary reward as compensation. The experiment was conducted in line with the principles expressed in the Declaration of Helsinki and received approval by the local ethics committee.

Apparatus and stimuli. All materials were identical to those used in Experiment 1. The visual properties of all stimuli were also identical to those used in Experiment 1; any differences are reported in the procedure.

Procedure. The procedure was similar to that of the first experiment. Each trial started with the presentation of a white central fixation cross, noise frame, and a grey-black textured occluder presented above fixation. This occluder was either opaque (Non-Occluded, Occluded) or semi-transparent (Induction). After 250ms the fixation cross was replaced with a white circle with a duration sampled from a uniform distribution ranging between 1000 and 1600ms. This test stimulus was either static, continuously modulated at 10 Hz, or modulated with a temporary disruption. This disruption occurred in line with the occlusion event, always starting and ending when the occluder fully overlapped with the stimulus. To avoid strong transients, the disruption always started and ended on the average luminance of the stimulus. This resulted in three temporal frequency profiles: Static, Continuous, and Disrupted. After a short delay (33, 67, 100 ms) the occluder moved downward (13.68°/s) going either in front (Occluded, Induction) or behind (Non-Occluded) the stimulus. After 217 ms the center of the occluder was aligned with the center of the screen. After the occluder had stopped moving, it maintained its position for 466–1133 ms depending on the duration of the stimulus and the starting delay. Following this period, the occluder moved up to its original position (at 13.68°/s) and remained on the screen. Participants reproduced the presented duration by pressing and holding the right arrow key. A new trial was initiated by pressing the spacebar.

Participants were tested in a 2 x 3 within-subject factorial design. The two factors were Occlusion (Non-Occluded, Occluded), and Temporal Frequency (Static, Continuous, Disrupted). Participants completed six blocks, with each block consisting of a single Temporal Frequency presentation and both occlusion conditions. The order of these blocks was counterbalanced across participants. Within each bock all combinations of the occlusion representations were counterbalanced and randomized across trials. Each blocked started with 25 repetitions of the two occlusion conditions (Non-Occluded, Occluded) as well as 25 Induction trials, followed by a further 50 repetitions of only the Non-Occluded and Occluded conditions. This resulted in a total of 50 trials for each unique combination between Induction trials and Temporal Frequency, and

150 trials for each unique combination with the Non-Occluded and Occluded conditions across the entire experiment. In total, participants completed 1050 trials spread over two 45-min sessions interrupted by a 15-min break.

Results & discussion

Because we presented randomly sampled durations between 1000 and 1600 ms, we first needed to calculate the reproduction error for each individual trial. To do this we calculated the ratio between the duration reproduced by the participants and the presented duration on each trial. Similar to the first experiment we then removed all individual trials with reproduction ratios two standard deviations larger or smaller than the mean for each condition, for each individual participant. This procedure resulted in the removal of 817 trials (3.71%). Next, we calculated the average reproduction ratio for each condition (Figure 4).

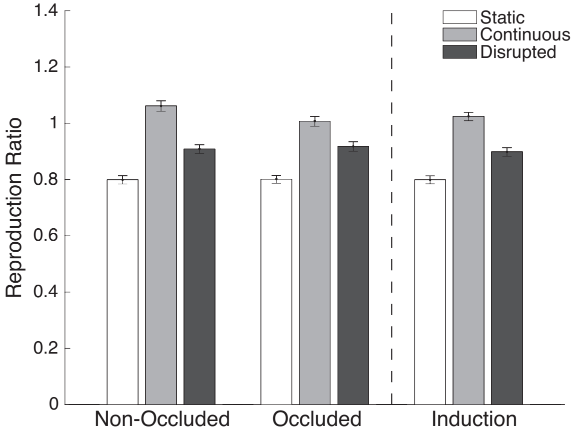


Figure 4. Average Reproduction Ratios, plotted separately for each Occlusion (Non-Occluded, Occluded, Induction) and Temporal frequency condition (Static, Continuous, Disrupted). Induction data were provided for transparency but are not analyzed in the manuscript. A reproduction ratio of 1 reflects veridical reproductions, with lower values reflecting underestimation and higher values reflecting overestimation. Error bars reflect within-subject standard errors.

The resulting data were analyzed in a 2 x 3 repeated-measures ANOVA with Reproduction Ratios as the dependent variable and Occlusion (Non-Occluded, Occluded) and Temporal frequency (Static, Continuous, Disrupted) as factors. As in Experiment 1 Greenhouse-Geisser corrections were used when the assumption of sphericity was violated. All post-hoc comparisons using t-tests were adjusted for multiple comparisons using the Holm-Bonferroni correction method (Holm, 1979). Corrected p-values are reported. Error bars in all images reflect within-subject standard errors, calculated using per-subject normalization of the data (Cousineau, 2005; Morey, 2008). Data for Induction trials were not analyzed here because we only collected one third of the data collected for the other Occlusion conditions, and because the results were not of our primary interest. A separate ANOVA was conducted for the Induction trials, which showed similar results to the data reported for the Non-Occluded condition.

We observed a main effect for Occlusion ($F(1,20) = 6.41$, $p < 0.020$, $\eta^2 = 0.24$) reflecting longer reproductions for the Non-Occluded compared to the Occluded stimuli. We also observed a main effect of Temporal Frequency ($F(2,40) = 29.638$, $p < 0.001$, $\eta^2 = 0.597$). Pairwise comparisons revealed that this main effect reflected shorter reproductions in the Static condition compared to both the Continuous and Disrupted conditions ($t(20) = -7.70$, $p < 0.001$ and $t(20) = -3.82$, $p < 0.001$, respectively). Furthermore, reproductions were longer in the Continuous condition compared to the Disrupted condition ($t(20) = 3.88$, $p < 0.001$). Finally, we observed a significant interaction between Occlusion and Temporal frequency ($F(2,40) = 34.46$, $p < 0.001$, $\eta^2 = 0.633$).

To better understand the interaction between Occlusion and Temporal Frequency we conducted a second analysis comparing the time dilation found for the Continuous and Disrupted conditions. We first calculated the percentage of time dilation for each Occlusion condition, for each participant (Figure 5). These data were then subjected to a 2 x 2 repeated-measures ANOVA with Time Dilation (%) as the dependent variable and Temporal frequency (Continuous, Disrupted) and Occlusion (Non-Occluded, Occluded) as factors. Results showed main effects for Temporal Frequency ($F(1,20) = 10.83$, $p = 0.004$, $\eta^2=0.351$) and Occlusion ($F(1,20) = 10.69$, $p < 0.004$, $\eta^2 = 0.348$). There was also a significant interaction between Temporal Frequency and Occlusion ($F(2,40) = 58.34$, $p < 0.001$, $\eta^2 = 0.745$) which seems to reflect a smaller difference between the Continuous and Disrupted conditions for the Occluded condition, compared to the Non-Occluded condition.

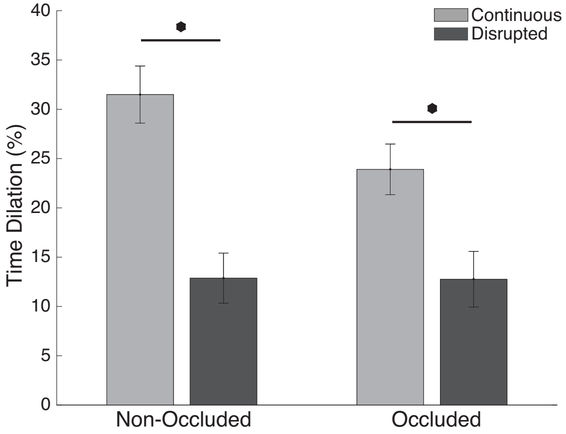


Figure 5. Average Time Dilation (%) for the Continuous and Disrupted presentations, plotted separately for each Occlusion condition (Non-Occluded, Occluded). Diamonds indicate significant deviation tested at an alpha of 0.05. Error bars reflect within-subject standard errors.

To further interpret this interaction we conducted two separate paired sample t-tests, one for each Occlusion condition. For the Non-Occluded condition we found larger time dilation for the Continuous condition compared to the Disrupted condition ($t(20) = 4.08$, $p < 0.001$). More importantly, for the Occluded condition we found the same result with larger time dilation in the Continuous condition compared to the Disrupted condition ($t(20) = 2.46$, $p = 0.023$). Since the Occluded version of the Continuous and Disrupted conditions were visually identical, this difference can only be explained by a difference in the representation of the stimulus during occlusion as a result of the different context in which they were presented. To further support the claim that these results reflect a difference in expected temporal frequency, we conducted a correlational analysis of the difference in Time Dilation between the Continuous and Disrupted conditions for the Non-occluded and Occluded conditions. We first calculated the difference in percentage of time dilation between the Continuous and Disrupted conditions. The resulting difference score reflects the time dilation that can only be explained by the difference in expected temporal frequency. We then correlated this Expectancy Effect for the Non-Occluded and Occluded conditions and found a strong correlation ($r = 0.93$, $p < 0.001$; Figure 6). This correlation supports the idea that participants' representation of the occluded stimulus is based on their non-occluded counterpart. Together, these results demonstrate that dynamic stimulus properties can be represented during occlusion, and that this representation can be modulated by expectations about the stimulus during the occlusion event.

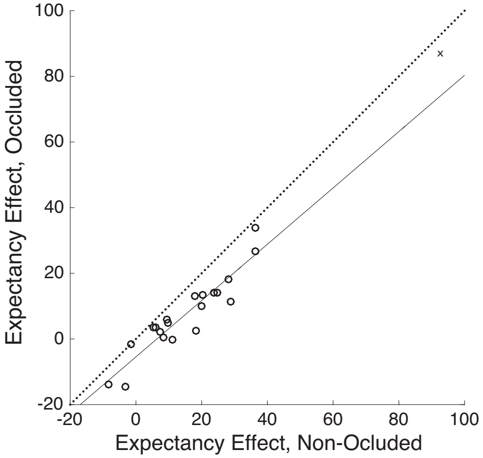


Figure 6. Scatterplot plotting the percentage of Time dilation that results from the difference in expected temporal frequency (Expectancy effect, %), for the Non-Occluded (x-axis) and Occluded (y-axis) conditions. Each open circle represents an individual participant. The x indicates an outlier (deviation >2*std), which was not included in the analysis. The dotted line indicates the regression line while the solid line represents the unity line.

General discussion

In this study we investigated whether dynamic stimulus information is represented during occlusion. To answer this question we used a well-known temporal illusion (temporal frequency induced time dilation) in which the perceived duration of a stimulus increases with an increase in temporal frequency content. We combined this illusion with a situation of stimulus occlusion to probe the representation of temporal frequency during occlusion. We hypothesized that if temporal frequency content is represented during occlusion it should affect judgments of duration made for temporarily occluded stimuli. To test this hypothesis we conducted two experiments.

In the first experiment, participants reproduced the duration of a stimulus that was either static or luminance-modulated (5 Hz, 10 Hz). During each presentation the stimulus either remained visible (Non-Occluded) or became temporarily occluded (Occluded). In a third, control condition (Extinction), the stimulus remained visible but its luminance modulation temporarily faded out, mimicking the loss of temporal frequency information in the occluded condition. This allowed us to dissociate between time dilation as a results of pre- and post- occlusion presentation of the stimulus and time dilation occurring during the period of occlusion. We observed clear time dilation, with longer reproductions for the luminance-modulated stimuli (5 & 10 Hz) compared to the static stimuli. Moreover, this effect was larger for the 10 Hz modulation compared to the 5Hz modulation. Furthermore, time dilation occurred in all three occlusion conditions, with the effect being larger for the Non-Occluded condition compared to the Occlusion and Extinction conditions. More importantly, time dilation was larger in the Occluded condition compared to the Extinction condition. This was true only for the 10 Hz luminance modulation, with no difference being observed for the 5 Hz modulation. This result indicates that the time dilation in the Occluded condition cannot be fully explained by the pre- and post- occlusion presentation of the stimulus. Instead, it argues for a representation of temporal frequency content during periods of occlusion.

In a second experiment we manipulated the expected temporal frequency of stimuli during occlusion by presenting occlusion events in different contexts of non-occluded presentations. These contexts consisted of blocked presentations of stimuli that were either static, continuously modulated at 10 Hz, or modulated at 10 Hz with a temporary disruption occurring in line with the occlusion event. The goal of these blocked presentations was to strengthen the assumption that the occluded stimulus had the same visual properties as its non-occluded counterpart. Since the disruption of temporal frequency content occurred during the occlusion of the stimulus, the continuous and disrupted modulations were visually identical when the stimulus became occluded. This allowed us to compare reproductions for occlusion events that were visually identical, but differed in the expected temporal frequency content of the stimulus during occlusion. We observed time dilation for the continuously modulated and disrupted stimuli, both when they were occluded as well as when they remained visible. We also observed larger time dilation for stimuli that were continuously modulated compared to the disrupted stimuli. This was true for the non-occluded presentations, which differed in their visual properties, but also for the occluded presentations, which were visually identical. Because the occluded presentations were visually identical, these observed difference between continuously modulated and disrupted stimuli cannot be explained by pre- and post- occlusion presentations of the stimulus. Together, these results demonstrate that dynamic stimulus properties can be represented during occlusion, and that this representation can be modulated by expectations about the stimulus during the occlusion event. Correlation analysis showed a strong correlation between time dilation for the non-occluded and occluded presentations, further supporting the notion that participants' representation of the occluded stimuli had similar properties as their non-occluded counterparts.

Our study provides the first evidence that dynamic stimulus properties other than changes in location are represented during occlusion. This shows that the representation of an occluded object can incorporate a wide range of information that has been accumulated over time and argues for a veridical representation of the visual features of the occluded object. The effect of temporal frequency on duration estimation during occlusion occurred even though the temporal frequency content of the stimulus was irrelevant for the completion of the task. This shows that dynamic properties of the stimulus can be represented automatically without any focused effort to maintain the information, similar to the results reported in earlier studies (Ban et al., 2013; M. M. Murray et al., 2006). Overall, these findings support the idea that observer maintain a rich, object-like representations of objects under occlusion based on the visual properties encoded during perception of the object before occlusion. Similar perception-like representations have been proposed and verified to underlie visual imagery (Bartolomeo, 2002; Johnson & Johnson, 2014), and visual working memory (Harrison & Tong, 2009). In general, findings from these domains support the view that internal representations of objects or events in the visual modality rely on a process of reactivation in visual areas that is highly similar to the activation observed during actual perception.

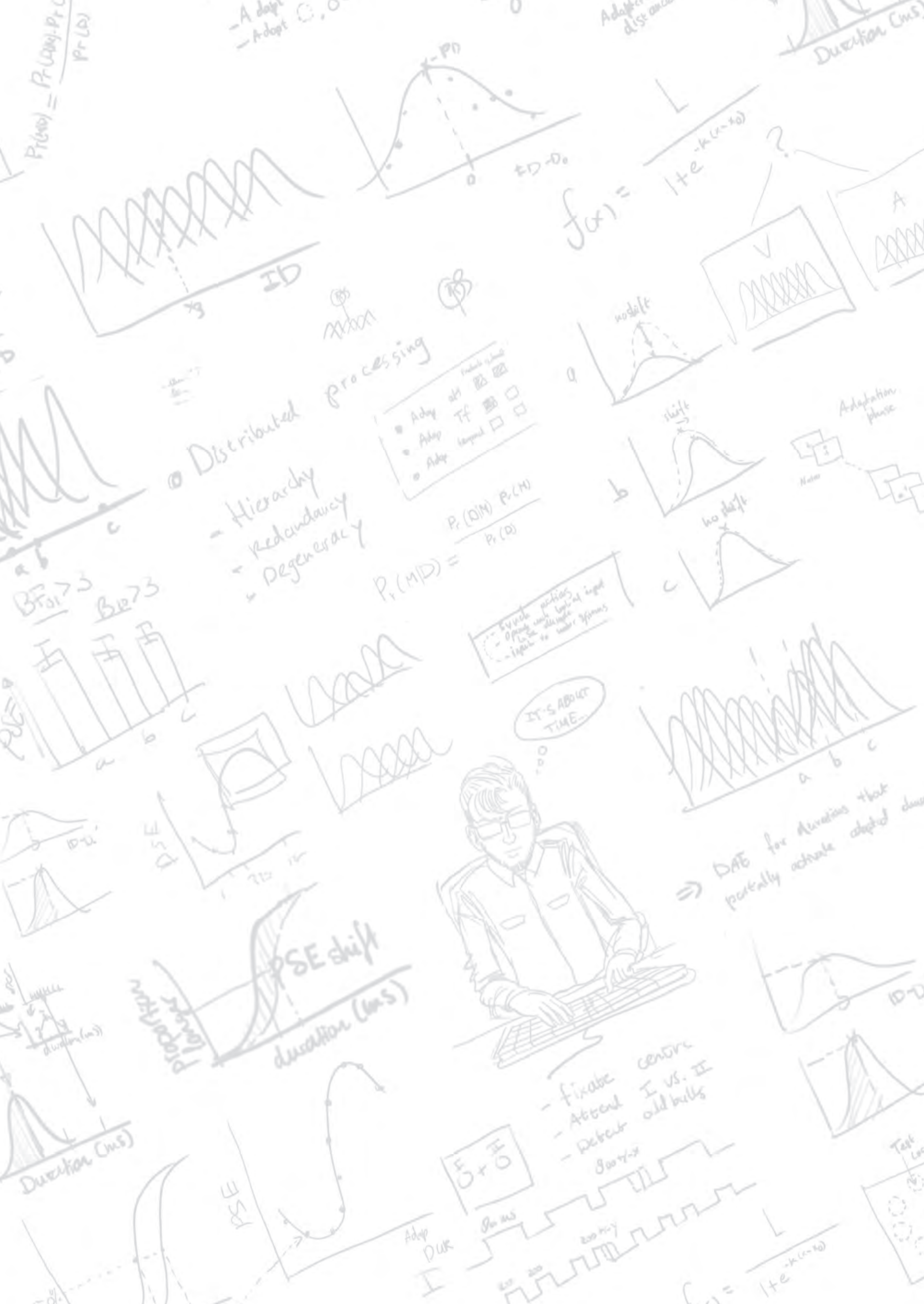
One possible concern about the results of Experiment 1 stems from the crucial comparison between the Occlusion and Extinction conditions. The goal of the Extinction condition was to mimic the loss in temporal frequency content, without the use of deletion and accretion cues that normally accompany occlusion events. This leads to a qualitative difference in the disappearance of the temporal frequency content between the two conditions. For the Occlusion condition the stimulus loses and gains contrast energy as a function of the spatial location of the occluder. For the Extinction condition the contrast energy fades linearly across the entire stimulus in the same time it takes the occluder to fully occlude the stimulus. These differences in the way temporal frequency content is removed could affect the perceived duration of the two events differently, compromising our comparison between the two conditions. When discussing these differences in the loss of temporal frequency content, it is important to stress that they pertain to the contrast energy of the stimulus that signals the temporal frequency, and not the temporal frequency itself. Several studies have shown that changes in temporal frequency content and speed can affect the perceive duration of an event (Bruno et al., 2012, 2015; Matthews, 2011). However, in our experiment the temporal frequency changes from 10/5Hz to static in both the Occluded and Extinction conditions. As such, these types of effects do not confound the data presented here. What does differ between these two conditions is the way in which the contrast energy of the stimulus decreases. Bruno and Johnston (2010) have shown that changes in contrast can lead to changes in the perceived duration of events. More specifically, they showed that a few seconds of adaptation to a high contrast stimulus with a temporal frequency of 10 Hz or higher resulted in compression of a subsequent interval compared to adaptation to a lower contrast. Since our stimulus loses contrast energy during occlusion/ extinction, similar compression of the occluded interval could occur. Given the qualitative difference between the two conditions, this compression could differ between the two occlusion conditions. However, it is unclear in what condition contrast adaptation would be higher, making it difficult to predict which interval would be compressed more. Moreover, since these compression effects are relatively small, ranging within the 10–20ms range for 10 Hz presentations after more than a second of adaptation, it is unlikely to explain the ~50ms difference in time dilation reported here.

A second possible issue with the difference in decrease of the contrast energy of the stimulus is that it could lead to a difference in the time point at which evidence for the presence of a 5/10 Hz signal falls below threshold. Plotting the total stimulus contrast as a function of time shows a linear pattern for the Extinction presentation and a pattern that approaches linearity for the Occlusion presentation (with slight deviations due to the stimulus being a circle, see Supplementary materials: Figure S1). Given the similar global spatiotemporal profiles of the two conditions and the relatively short occlusion period (133 ms, ~0.65/1.3 cycles for the 5/10 Hz presentations), it seems unlikely that the time point at which the stimulus is viewed as no longer flickering is very different between the Occlusion and Extinction conditions. As a result, any difference in the total on-period of the temporal frequency signal should be relatively small and will not lead to any substantial shifts in the perceived duration of the pre- and post- occlusion segments of the Occlusion condition compared to the Extinction condition. Any differences that do occur are unlikely to account for the twofold increase in the magnitude of the duration illusion observed between the Occluded (102 ms, 60% remaining of the illusion found for non-occluded presentation) and Extinction (56 ms, 33% remaining of the illusion found for non-occluded presentation) presentations in the 10 Hz conditions. This conclusion is further supported by the fact that the effect of temporal frequency content on duration tends to plateau for longer durations. The initial presentation of the temporal frequency signal causes the largest amount of dilation, with only a small, non-linear added dilation effect resulting from an increase in the duration of the event (Kanai et al., 2006). To conclude, while the Occluded and Extinction condition differ in their visual properties, these differences are unlikely to explain the reported difference between the Occlusion and Extinction conditions.

In Experiment 1, we did not find evidence for the representation of temporal frequency content during occlusion for stimuli modulated at 5 Hz. One possible explanation for this result is the smaller time dilation effect for the non-occluded presentations of the 5 Hz stimuli. Less time dilation for non-occluded stimuli predicts smaller amounts of time dilation in the occluded and extinction presentations, which could result in smaller differences between the two conditions that can no longer be detected in the noise of participants' performance. Alternatively, the lack of time dilation for 5 Hz modulation could be explained by the lower sensitivity to 5 Hz stimulation compared to 10 Hz stimulation. Earlier work has shown that human observers are most sensitive to temporal frequencies ranging between 8 and 12Hz (Kelly, 1961; Shady, MacLeod, & Fisher, 2004). This difference in the encoding of the information could results in a weaker representation of the temporal frequency information, explaining the lack of an effect in the 5 Hz condition. Finally, it has been documented that higher contrast in temporal frequency content between stimuli capture attention (Cass, Van der Burg, & Alais, 2011). In our experiment the difference in temporal frequency content between the stimulus and the static background is much larger in the 10 Hz condition than it is in the 5 Hz condition. Similar to the previous point, such a difference could lead to less effective encoding of the temporal frequency content of the stimulus, resulting in a smaller/no effect for stimuli with a lower temporal frequency content. Within the current design it is not possible to validate or dissociate any of these explanations.

Previous experimental work examining the relative contribution of spatio-temporal versus feature information has shown that both can be used to establish object correspondence during occlusion events (Flombaum et al., 2009; Hollingworth & Franconeri, 2009; Moore et al., 2010). However, tracking combinations of feature and location information seems to be an effortful process with a limited capacity (Cohen, Pinto, Howe, & Horowitz, 2011; Saiki, 2003). As a result, it seems that spatiotemporal information is often prioritized over feature information even when both are available (Flombaum et al., 2009; Kimchi & Pirkner, 2014; Scholl, 2007). Furthermore, the extent to which each of these types of information is used seems to depend on the informativeness and reliability of each source of information (Hein & Moore, 2012; Papenmeier, Meyerhoff, Jahn, & Huff, 2014). In the current study, the location of the stimulus was constant throughout the experiment. This lack of change in the spatial location of the stimulus decreases the relevance of this information and lowers the need for integration of spatio-temporal and feature information. It is unclear how the addition of locational change would influence the representation of the dynamic feature properties of an object. Most likely, a similar prioritization of spatio-temporal information will be observed. Alternatively, the temporal component of feature change could increase the informativeness of an objects features resulting in increased prioritization of the feature information. Investigating this interaction could further inform theories about the importance of the temporal components of feature and location information in the prioritization of spatio-temporal information.

This study focused on temporal frequency as a dynamic object property. However, information about dynamic properties like temporal frequency and speed are derived from other sources of visual information. In our study, temporal frequency content is derived from the rate of luminance change over time. However, other changes – such as changes in color under conditions of equiluminance – also convey temporal frequency information. This raises an interesting question about the way by which temporal frequency information is represented during occlusion. One possibility is that the information is represented in neurons encoding the actual changes in luminance. Luminance and contrast sensitive neurons in lower level visual areas have been shown to possess selectivity for a wide range of temporal frequencies (Foster, Gaska, Nagler, & Pollen, 1985; Singh, Smith, & Greenlee, 2000) and as such can represent both the changes in luminance as well as the resulting temporal frequency. However, since temporal frequency selective neurons are present throughout the visual cortex (D'Souza, Auer, Strasburger, Frahm, & Lee, 2011; Fawcett, Barnes, Hillebrand, & Singh, 2004; McKeeff, Remus, & Tong, 2007; Singh et al., 2000) it is also possible that this information is represented in other visual areas, independent of the signal that defines the temporal frequency content. Previous work has already shown that information about motion is represented as both locational changes over time (Ban et al., 2013) as well as its velocity derived from this locational change (Olson et al., 2004), showcasing this possible distinction. Whether a similar redundancy occurs for the representation of dynamic stimulus properties such as temporal frequency remains an interesting topic for future study.


Distributed processing
- Hierarchy
- Redundancy
- Degeneracy
$P_r(M|D) = \frac{P_r(D|M)\,P_r(M)}{P_r(D)}$
$f(x) = \frac{L}{1+e^{-k(x-x_0)}}$
IT'S ABOUT TIME...
PSE shift
duration (ms)
Proportion longer
no shift
shift
no shift
a
b
c
PSE
ID
Adaptation phase
=> DAE for durations that partially activate adapted durations
- fixate centre
- Attend I vs. II
- Detect odd bulb
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Duration (ms)
BF₀₁>3
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PD
ID-D₀
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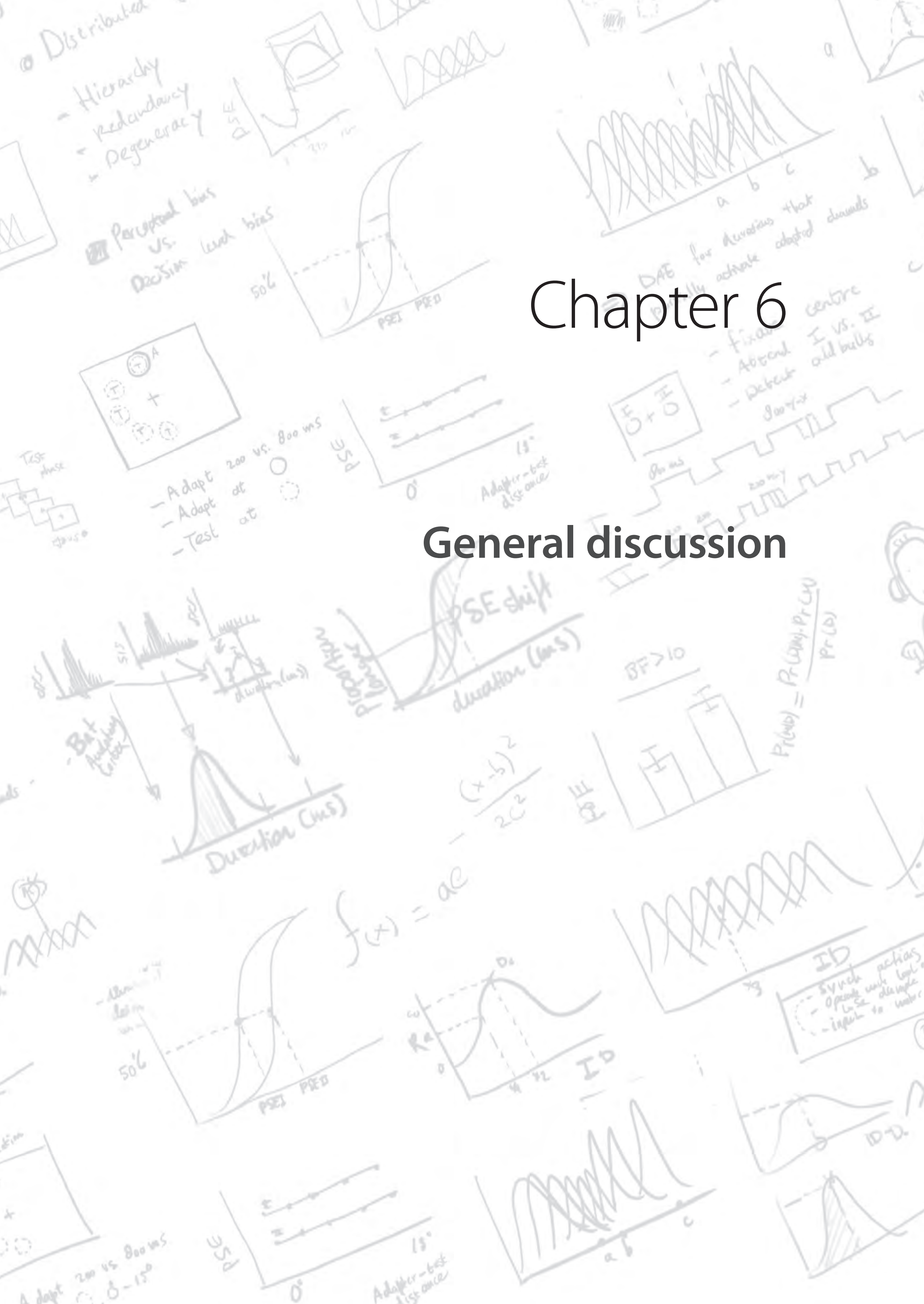


Chapter 6

General discussion

General discussion

The overall aim of the work presented in this dissertation was to better understand the way in which we extract temporal information from the world around us, and how we use that information to guide our behavior. In chapters 2, 3, and 4 we focused on duration processing and the way in which duration information is extracted from visual information. We used the duration channel model as our theoretical framework and utilized sensory adaptation to probe the encoding of duration. By doing so, we aimed to test several assumptions of the duration channel model as well as to more clearly define the model's position within the existing literature. In chapter 5, we studied the representation of temporal information during occlusion.

In the following segments I will briefly discuss the main findings of each chapter and provide an overall conclusion. Following that, I will discuss theoretical implications, caveats, and possible future directions of research.

The perception of duration

In **Chapter 2**, we studied the relative position of duration-tuned mechanisms along the visual processing hierarchy. To this end, we measured the spatial selectivity of the duration after-effect (DAE) following adaptation. The area of visual space over which sensory information is integrated increases along the visual processing hierarchy (A. T. Smith et al., 2001). As a result, after-effects that are caused by adaptation early on in the visual processing hierarchy are confined to relatively small areas of visual space around the adapted location. In contrast, after-effects that are the result of adaptation at later stages of visual processing do not show such spatial restrictions. From this, we hypothesized that if the encoding of duration occurs early in the visual processing hierarchy, the DAE should be restricted to an area within a few degrees of visual angle from the adapted location. Conversely, if duration information is encoded later on in the visual processing hierarchy, the DAE should remain relatively similar in magnitude across visual space. We found clear evidence for a DAE at all measured distances from the adapted location (0-15° of visual angle), with no evidence for a decrease in the magnitude of the DAE at larger distances or across hemifields. We concluded that duration information is a stimulus property that is encoded relatively late in the visual processing hierarchy.

The results from chapter 2 provided a strong starting point for our subsequent studies. Most directly, the lack of spatial selectivity allowed us to manipulate the spatial location of adaptation stimuli, which increased our options in designing the paradigms used in chapter 3 and 4. More importantly, the results reported in chapter 2 raised several questions that were fruitful for discussion and in planning our future studies.

First, it remained unclear how our findings relate to behavioral work which has demonstrated modulation of duration perception following adaptation to other temporal and non-temporal stimulus features on perceived duration (Johnston et al., 2006; Ortega et al., 2012; Zhou et al., 2014). These studies report strong spatial selectivity, indicating an origin in early visual areas (e.g. V1). This suggest that duration perception relies on distinct process and raises questions about *why* multiple process might exist and *if* and *how* they might interact. These questions are discussed further in a later segment in this chapter titled 'Unifying theories of duration perception' (page 119). Second, the lack of spatial selectivity raised questions about the selection and processing of multiple sources of duration information. Everyday interactions with the environment will often contain multiple events happening in close (or even overlapping) spatial and temporal proximity. The lack of spatial selectivity in the duration-tuned mechanisms means that duration information is integrated across large areas of visual space and cannot be segregated on the basis of spatial location. Given this lack of segregation based on spatial location, it is unclear how duration-tuned mechanisms deal with the presentation of multiple sources of duration information. One potential solution lies with our ability to use visual attention to select relevant information against concurrently presented, irrelevant information. At a neuronal level, this property is reflected by a decreased relative response to unattended vs. attended features presented within the receptive field of a single neuron (Chelazzi et al., 1998; Moran & Desimone, 1985; Reynolds & Chelazzi, 2004; Reynolds et al., 1999; Suzuki, 2001). This means that attention can allow for the selective encoding of duration even when competing sources of duration information are presented in close spatial proximity.

In **Chapter 3**, we used duration adaptation to investigate the role of attention in the selective encoding of duration when multiple sources of duration information are present. We measured the DAE following adaptation to two simultaneously presented streams of duration information. In each case only one of the streams was relevant to the participant's task, requiring attention to be directed towards that stream. We then measured the relative contribution of attended versus unattended duration information to the DAE. We found that only the attended durations contributed to the measured DAE, with no contribution for the unattended durations. These results demonstrate that attention plays a crucial role in the selective encoding of duration: attended durations are encoded, while encoding of unattended durations is either weak or absent. We concluded that visual attention underlies the selection of relevant temporal information when multiple sources are present.

This strong role of attentional selection in duration encoding also supported our conclusion from chapter 2 about the relative position of duration-tuned mechanisms in the visual processing hierarchy. It is known that the magnitude of attentional modulation of neural responses to a certain feature changes as a function of the complexity of that feature as well as its position in the visual processing hierarchy (Suzuki, 2001). Since we found no evidence for a significant contribution of the unattended duration to the measured DAE, our results from chapter 3 support our conclusion that duration is a complex feature encoded by mechanisms located at higher-level areas of the processing hierarchy.

The results of chapter 3 also raised questions about the nature of attentional selection and the source of information being selected to extract duration information. The clear role for attention in the selective encoding of duration suggests that duration encoding is subject to the capacity limits of the attentional system. In line with this suggestion, several studies have reported behavioral detriments when processing multiple, temporally overlapping durations (Ayhan et al., 2012; Cheng et al., 2014; Morgan et al., 2008; van Rijn & Taatgen, 2008). Interestingly, this capacity limit seems to be associated with the amount of temporal overlap between the onsets and offsets of the different stimuli (van Rijn & Taatgen, 2008). This suggests that stimulus onsets and offsets provide key information necessary to encode the duration of events. In chapter 4 we investigated the role of onset-offset information as a source of information used to encode duration.

In **Chapter 4**, we combined adaptation with a temporal illusion to investigate the nature of the signal encoded by duration-tuned mechanisms. Some specific temporal illusions have been shown to lead to increases in perceived event duration, without changing the perceived onset or offset of that same event (Kaneko & Murakami, 2009). This dissociation between signal length and perceived duration posed an interesting question about which information is being used to extract the feature of duration. Within the duration channel model it is assumed that onset-dependent offset responses underly the tuned neural responses in the duration channels. However, if duration channels are responsible for the encoding of duration, one would expect the population response within the duration channels to reflect the duration eventually perceived by the observer. By adapting observers to a temporal illusion which dissociates perceived signal length and perceived duration, we could measure whether duration channels encode duration based on the length of the sensory signal (onset-offset duration) or whether the encoded duration reflected the duration perceived by the observer. We found that observers adapted to the *onset-offset* duration, and not to a duration corresponding to the *perceived duration* of the illusion-inducing stimulus. From this, we concluded that channel-based duration encoding reflects the temporal distance between the onset and offset of an event and does not necessarily correspond to the perceived duration of that same event. While this conclusion is in line with the assumptions of the duration channel model, it remains surprising that the duration channels do not encode a duration that corresponds to the duration perceived by the observer. Similar to our suggestion in chapter 2, this result implies that duration perception does not rely solely on processing by duration channels. Instead it seems that duration perception is either informed by multiple stages of processing or by multiple distinct processes.

The results of chapter 4 demonstrate an important role for stimulus onsets and offsets in duration encoding. In other words, the ability to effectively encode duration information for multiple events seems to rely on the processing of the events' onsets and offsets. Interestingly, this also suggests that processing the entire interval might not be needed and that attending the on- and offset of an interval could be sufficient to encode its duration. Together with Chapter 3's results, this underscores the notion that duration encoding is an effortful process which relies on the successful selection of onset and offset information to encode relevant duration information.

Finally, the fact that the temporal illusion studied in chapter 4 does not affect the encoding of duration by duration-tuned mechanisms should prompt us to be cautious about attributing temporal illusions to specific changes in duration encoding. Historically, the occurrence of temporal illusions has been a fertile ground for speculations about the mechanisms underlying duration encoding. In particular, duration illusions are often assumed to reflect direct changes in the encoding process (i.e. changing the clock speed), and as such have frequently been used to study the mechanisms underlying the encoding of duration information from sensory information (e.g. Droit-Volet & Wearden, 2002; Eagleman, 2008; Kanai et al., 2006; Pariyadath & Eagleman, 2007; Xuan et al., 2007). The Temporal Frequency Induced Time Dilation (TFITD) illusion used in chapter 4 is a good example of this, since it is assumed to reflect changes in the rate at which temporal information is accumulated during duration encoding (Kanai et al., 2006). In contrast with this assumption, our results suggest that the TFITD illusion does not affect the (channel-based) encoding of duration and likely reflects modulation during subsequent processing. This suggestion is similar to reports demonstrating that the effects of stimulus size and numerosity on duration perception occur during the maintenance of duration information in memory, instead of during duration encoding (Cai & Wang, 2014; Rammsayer & Verner, 2015). While the results reported in chapter 4 only concern a single temporal illusion, our findings do call into question the extent to which duration illusions reflect direct changes in the encoding of duration information.

The perception of temporal frequency

In chapter 5, we focused on a different topic: the encoding and maintenance of temporal information during occlusion. It is well documented that human observers maintain a representation of the visual features of objects when these objects become occluded. These internal representations allow observers to extrapolate events occurring during occlusion and quickly identify objects upon reappearing. Earlier work has focused mostly on the representation of static properties of objects under occlusion. However, in many situations visual features change as a function of time. Representing these changes, and the rate at which they occur, could provide additional benefits for extrapolation during occlusion and identification of objects upon reappearance. In chapter 5, we investigated whether information about the rate of change of visual information is also represented during occlusion. We used the TFITD illusion in which the perceived duration of an event increases as a function of its temporal frequency content (Kanai et al., 2006). By combining this illusion with a situation in which the object becomes occluded, we could investigate the effect of temporal frequency content on the perceived duration of the occluded stimulus. If the temporal frequency content of the illusion-inducing stimulus is represented during occlusion, it should still influence the perceived duration of the event even when that object is no longer visible. In two experiments we found that (expected) temporal frequency content influenced the perceived duration of a stimulus while it was occluded. From this, we concluded that the representations of occluded objects contain a wide range of features derived from the period when the object was still visible, including information about both the static and dynamic properties of the object. Interestingly, the results reported in Chapter 5 also underscore the role of temporal frequency as an integral component of our perception of duration. Even under conditions when information about change is no longer present, a representation of this information is actively maintained and used to inform our perception of duration.

Summary

To summarize, we demonstrated that duration-tuned mechanisms: are located at a relatively late stage in the visual processing hierarchy (Chapter 2); rely on attention to effectively select duration information when multiple source of duration information are present (Chapter 3) and; encode duration based on the length of the sensory signal (Chapter 4). We conclude that duration is a high-level stimulus feature which is encoded via an effortful process which relies on attention to select relevant onset and offset information to encode duration. Together these studies demonstrate the value of using sensory adaptation and the duration channel model as a guiding framework for studying the encoding of duration. In addition, we demonstrated that temporal information is maintained during conclusion and discussed the importance of temporal frequency as a source of temporal information (chapter 5). In the following sections, we will discuss theoretical considerations and outstanding issues that are relevant for future research. Since the bulk of this dissertation focuses on duration perception, this discussion will focus on critically evaluating the role of the DAE and the duration channel model in studying and understanding the encoding of duration.

On measuring the DAE to study duration encoding

The studies reported in chapters 2, 3 and 4 rely heavily on the assumption that the DAE reflects selective adaptation of duration-tuned channels as a result of the repeated encoding of their preferred duration. In each chapter, differences in DAE magnitude were taken to reflect changes in the encoding of information and were used to draw conclusions about the neural underpinnings of duration encoding. Here I will discuss the possibility that the DAE could reflect both a sensory bias and a decisional bias. Secondly, I will discuss the relation between the DAE and the neurophysiological work demonstrating tuned neural responses.

Perceptual bias vs. decision level bias

One common concern in measuring the behavioral consequences of sensory adaptation is that it can be challenging to distinguish changes in observers' perception of the stimulus (sensory bias) from changes in their reporting behavior (decision level bias) (Linares & Gorea, 2015; Mather & Sharman, 2015). As described throughout this dissertation, after-effects following sensory adaptation (e.g. tilt after-effect, motion after-effect, duration after-effect) are often assumed to reflect changes in the neural responses of feature-tuned neurons that code for the adapted feature value. This change in neural responses causes a shift in the relative activation of groups of feature-tuned neurons, which in turn leads to shifts in the encoded feature value causing changes in observer's perception of that feature. In contrast, it could be argued that behavioral changes following adaptation result from changes to the decision-making involved in sensory decision-making tasks (Mather & Sharman, 2015). This type of decision level bias is characterized by a change in the way that sensory evidence is evaluated (i.e. criterion shift) in order to make a perceptual decision. These decision level biases could occur as a form of recalibration or error-correction when faced with the heavily skewed presentations that are part of an adaptation procedure (i.e. repetitions of a single duration). Sudden changes in the distribution of duration information can reflect a bias in external stimuli, but can also reflect changes in sensory processing or the occurrence of coding errors. As such, the sudden changes introduced by the adaptation procedure could lead to normalization of sensory decisions by relabeling the input from sensory mechanisms in an effort to maintain consistency with previous experiences. This relabeling changes the interpretation of future input, which manifests itself in an unconscious or conscious shift in participants' responses to the test stimulus used to measure the consequences of the adaptation procedure (Mather & Sharman, 2015).

Both the sensory and decision level biases described above result in a pattern of behavior in which test stimuli are reported as more distinct from the adapted duration. Given that the conclusions drawn in chapter 2, 3, and 4 are based on the idea that the DAE reflects changes in the neural responses of feature-tuned neurons (sensory bias), a strong decision bias component to the DAE would undermine our methods and results. In most published work, including our own, the occurrence of decision level biases in the duration adaptation paradigm is not actively prevented or quantified. Despite this lack of intentional control for decision level biases, there are several arguments that can be made, based on current methodology and empirical findings, against the occurrence of a (primarily) decision level bias in the DAE.

Firstly, the cross-modal duration judgement task used in our paradigm provides a distinct reference against which the test stimulus is judged. Decision level biases are most prevalent in paradigms using the method of single stimuli (García-Pérez & Alcalá-Quintana, 2013; Morgan, Dillenburger, Raphael, & Solomon, 2012; Storrs, 2015). In these tasks, participants classify a test stimulus as belonging to one of two categories. Without a sensory reference, this classification is based on an internal reference derived from the overall experience of duration in the context of the experiment. This type of internal reference is more likely to be influenced by the recent sensory experience provided by the adaptation stimuli (García-Pérez & Alcalá-Quintana, 2013; Storrs, 2015). In contrast, the 2AFC task used in our experiments employs a cross-modal duration judgment in which the reference stimulus consists of an auditory stimulus that is unaffected by the adaptation protocol (Heron et al., 2012). This encourages participants to judge test stimuli against the presented auditory reference durations, and not on the visual adaptation presentations. As such, our method should be less susceptible to decision level bias.

A second argument against the presence of a decision level bias in the DAE comes from the fact that the DAE consists of a temporally localized repulsion of perceived duration. The magnitude of the DAE increases as a function of the difference between the adapter and the test stimulus. However, as the adapter-test difference becomes too large, the magnitude of the DAE decreases, with responses eventually returning to baseline (Heron et al., 2012; Chapter 1, Figure 4). This pattern of results is consistent with temporally localized sensory adaptation, which only affects the subsequent encoding of similar durations. In contrast, a decision level bias as a result of the recalibration of responses would occur at all adaptation durations regardless of the difference between the adapted and tested duration. As such, these results argue against a purely decisional bias account of the DAE.

A final argument against the presence of a decision level bias in the DAE comes from the reported dissociations between the perceived duration of a stimulus, and the DAE measured following adaptation to that same stimulus (Heron et al., 2013, Chapter 4). If decision level biases reflect recalibration of responses based on earlier evaluations of sensory input (Mather & Sharman, 2015), one would expect a decision level bias to occur based on the durations available for decision (i.e. the durations perceived by the observer). In Chapter 4, we adapted observers to an illusion-inducing stimulus and found no evidence that they adapted to the duration corresponding to the perceived duration of that stimulus. Instead, we found that the DAE reflected adaptation to the temporal distance between the on- and offset of an event (onset-offset duration). Similarly, Heron and colleagues (2013) adapted observers to multimodal stimuli for which the perceived duration of the visual component was shifted towards the duration of the auditory component. In contrast to this shift in perceived duration, adaptation to these same stimuli resulted in adaption to the duration of the visual component and not the duration perceived by the observer. Both these studies demonstrate a dissociation between perceived duration and the duration adaptation reflected by the DAE. These patterns of results are unlikely to result from decision level bias as the information available for decision (and recalibration) and the duration to which observers adapt are different.

While the arguments presented above provide converging evidence against a strong role for decision level bias in the DAE, they do not exclude the occurrence of a decision level biases from contributing to the DAE per se. One approach to further address this issue would be to design experimental methods that aim to reduce decision level bias (Mather & Sharman, 2015; Storrs, 2015). For example, by using altered variations on the nAFC paradigm to manipulate decision level bias (García-Pérez & Alcalá-Quintana, 2013; Jogan & Stocker, 2014; Morgan, 2013, 2014). Alternatively, paradigms could aim to measure adaptation-associated changes in sensitivity instead of changes in the PSE, which should not be susceptible to decision level changes (Clifford, Wyatt, Arnold, Smith, & Wenderoth, 2001; Kohn, 2007; Morgan, Chubb, & Solomon, 2006). While these methods provide valuable tools to manipulate, measure, and reduce the contribution of decision level bias, it is not always possible or practical to transfer these methods to the domain of temporal judgements. For example, some improved variations of nAFC tasks require concurrent presentation of multiple reference-test pairs which is not possible when studying duration (Jogan & Stocker, 2014; Morgan, 2014).

Instead of using an nAFC, a more valuable approach could be to use experimental methods that allow for the dissociation and quantification of changes in perceptual evidence (perceptual bias) and changes in decision criterion (decision level bias). One example of such a method would be to quantify different changes in perceptual decision-making by modeling decision-making data using a drift diffusion model (DDM). DDMs assume that a dichotomous decision-making process is characterized by the accumulation of evidence until a certain decision threshold is reached (Forstmann, Ratcliff, & Wagenmakers, 2016; Ratcliff, 2014; P. L. Smith, 2000). The higher the quality of the sensory evidence, the higher the rate at which evidence can be accumulated (drift rate). In addition, changes in decision threshold can also affect the probability that a certain decision is reached. This distinction between drift rate and decision threshold is analogous to the perceptual and decision level biases described earlier. If duration adaptation causes test stimuli to be perceived as more distinct from the adapted duration (perceptual bias) it should lead to a predictable increase in discriminability for certain perceptual decisions (i.e. increase in drift rate). Conversely, decision level biases would manifest themselves as shifts in the relative distance to the two decision thresholds. By modeling both decisions and the associated response times, drift diffusion models can be used to understand the relative contribution of changes in drift rate and changes in thresholds to observed changes in decision making. By taking advantage of this characteristic, drift diffusion models could provide new insight into the prevalence of both perceptual and decision biases in the DAE.

Relating behavioral outcomes to neurophysiological processes

Throughout this dissertation, I discussed two main categories of evidence that support the notion that duration-tuned responses play a role in our capacity to encode duration. First, I discussed the existence of tuned behavioral responses such as the DAE which occurs after sensory adaptation (Heron et al., 2012). I argued that the occurrence of tuned behavioral responses reflects the existence of duration-tuned neural structures. Secondly, I discussed evidence for the existence of duration-tuned neural responses in different areas of the brain, measured in both humans (Hayashi et al., 2015, 2018; Protopapa et al., 2018) and non-human animals (Duysens et al., 1996; Ehrlich et al., 1997; He & Hashikawa, 1998; Merchant, Pérez, et al., 2013; Mita et al., 2009). These results demonstrate that humans possess neural substrates that could underly the reported tuned behavioral response, providing a possible mechanism for duration encoding.

Given the parallel between these two sets of results, it seems likely that tuned behavioral responses reflect a behavioral consequence of processes occurring in duration-tuned neural structures. However, there is no direct evidence linking tuned behavioral responses to the tuned responses observed in neurophysiological recordings and neuroimaging studies in humans. Without direct evidence linking the two, it is possible that the observed tuned behavioral responses occur independently of the reported tuned neural responses (Teller, 1984). To address this issue, future work should aim to measure the effects of adaptation on both neural responses and behavior concurrently. For example, by combining fMRI decoding of duration with adaptation paradigms it should be possible to demonstrate changes in neural responses following duration adaptation while also showing that these changes have predictive value for subsequent duration judgements. Alternatively, studies could aim to directly affect the responsiveness of duration sensitive neural structures (e.g. lesion studies in non-human animals, rTMS in human observers) and measure the consequences on timing behavior. By incorporating these techniques into the study of duration perception it should be possible to provide stronger evidence for the assumed causal relation between duration-tuned neural responses and tuned behavioral responses.

Unifying theories of duration perception

The studies described in chapters 2,3 and 4 of this dissertation focussed strongly on the framework of channel-based duration encoding. This strong focus on a single framework raises the question as to why there is no discussion of our results in terms of other models of duration perception. The main reason for this lack of a discussion is the fact that the duration channel model is the only theoretical framework that predicts the occurrence of the DAE. No other model allowed us to make predictions about the DAE or interpret our experimental results. Unfortunately, this lack of conceptual overlap between different models and experimental results is rather common in the domain of duration perception. In many cases, theories are only used to provide post-hoc explanations for standard timing behaviour (e.g. Vierordts law; Vierordt, 1868) or novel experimental results (i.e. different temporal illusions). The mechanisms used to provide these explanations are sometimes overly powerful, with no room for falsification. The most notable example of this is the clock model's explanation for unidirectional changes in perceived duration being the result of the 'clock' or accumulator speeding up or slowing down. While changes in clock speed do provide an explanation for unidirectional changes in perceived duration, it lacks a mechanistic description as to why certain factors would influence the speed of the clock. Another issue is that many predictions that are made by existing models, are highly specific for that particular theory with no comparable predictions being made by other models. The DAE is a good example of a key finding supporting a certain model that has no explanation within any of the other models.

From the above, it should be clear that the different models of duration perception make only few predictions, with opposing predictions arising from different models being extremely rare. To the best of my knowledge, there isn't a single article that contrasts predictions made by two models of duration perception that rely on a distinct mechanism and tested them empirically. This general lack of a conceptual overlap between different models and experimental results makes it difficult to critically compare and evaluate the different models.

In the following section I will discuss my view on this issue as it pertains to the duration channel model and the duration perception literature as a whole. First, I will briefly underline the specificity of the duration channel model in its current form. Next, I will talk about my view on building towards a more comprehensive theory of duration perception. In particular, I will discuss the importance of embracing the multi-faceted nature of timing behaviour and the proposal that duration perception might rely on a distributed processing network.

Broadening the scope of the duration channel model

Until recently, the number of studies on the duration channel model was limited. In most cases, studies focused on providing additional evidence for the role of duration-tuned mechanisms in duration encoding (i.e. DAE, duration specificity in learning, duration-tuned neural responses). Some other studies have also focused on identifying key properties of the duration channels such as feature specificity (Li, Yuan, & Huang, 2015), modality specificity (Heron et al., 2012, 2013), processing locus and hierarchy (Fulcher, McGraw, Roach, Whitaker, & Heron, 2016; Heron, Fulcher, Collins, Whitaker, & Roach, 2019; Li, Yuan, Chen, Liu, & Huang, 2015; Chapter 2), and sub- vs. supra-second duration processing (Shima et al., 2016). Having said this, there is a wide range of topics that are typically considered in the timing literature (see for reviews: Allman, Teki, Griffiths, & Meck, 2014; Eagleman, 2008; Grondin, 2010) that have not been discussed in terms of its relation to the duration channel model. For example, it is unclear what exact role duration-tuned mechanisms play in the overall production of timing behavior. While the duration channel model focusses mainly on the encoding of duration, there is no consensus as to whether duration-tuned mechanisms also play a role in the maintenance of duration information, comparisons between durations, or the production of duration or other timed behavior. In addition, it is unclear whether duration channels underlie the encoding and processing of different types of duration judgements such as prospective vs. retrospective duration judgements or implicit vs. explicit duration judgements.

In addition, there is a wide range of temporal illusions described in the literature that cannot readily be explained by the duration channel model in its current form. Examples of this include duration compressions resulting from eye-movements (Morrone, Ross, & Burr, 2005), effects of repetition and predictability on perceived duration (Pariyadath & Eagleman, 2007; Tse et al., 2004; Ulrich et al., 2006), duration compression following adaptation to visual features (Johnston et al., 2006; Zhou et al., 2014), the impact of temporal context on timing behavior (Jazayeri & Shadlen, 2010; Roach et al., 2017), and interactions between duration and other magnitudes (Xuan et al., 2007). These limits in the scope of the duration channel model raise questions about the applicability of the duration channel model to timing behavior in a broader context. As with any new model, an important next step will be to evaluate the model in light of the existing literature to fully understand the role of duration-tuned mechanism in duration perception on a wider scale. Future work should aim to further formalize the duration channel model so that it allows for more precise predictions about timing behavior in novel circumstances while at the same time allowing for more direct comparisons with the existing literature.

Consolidating the duration channel model with other models of duration perception

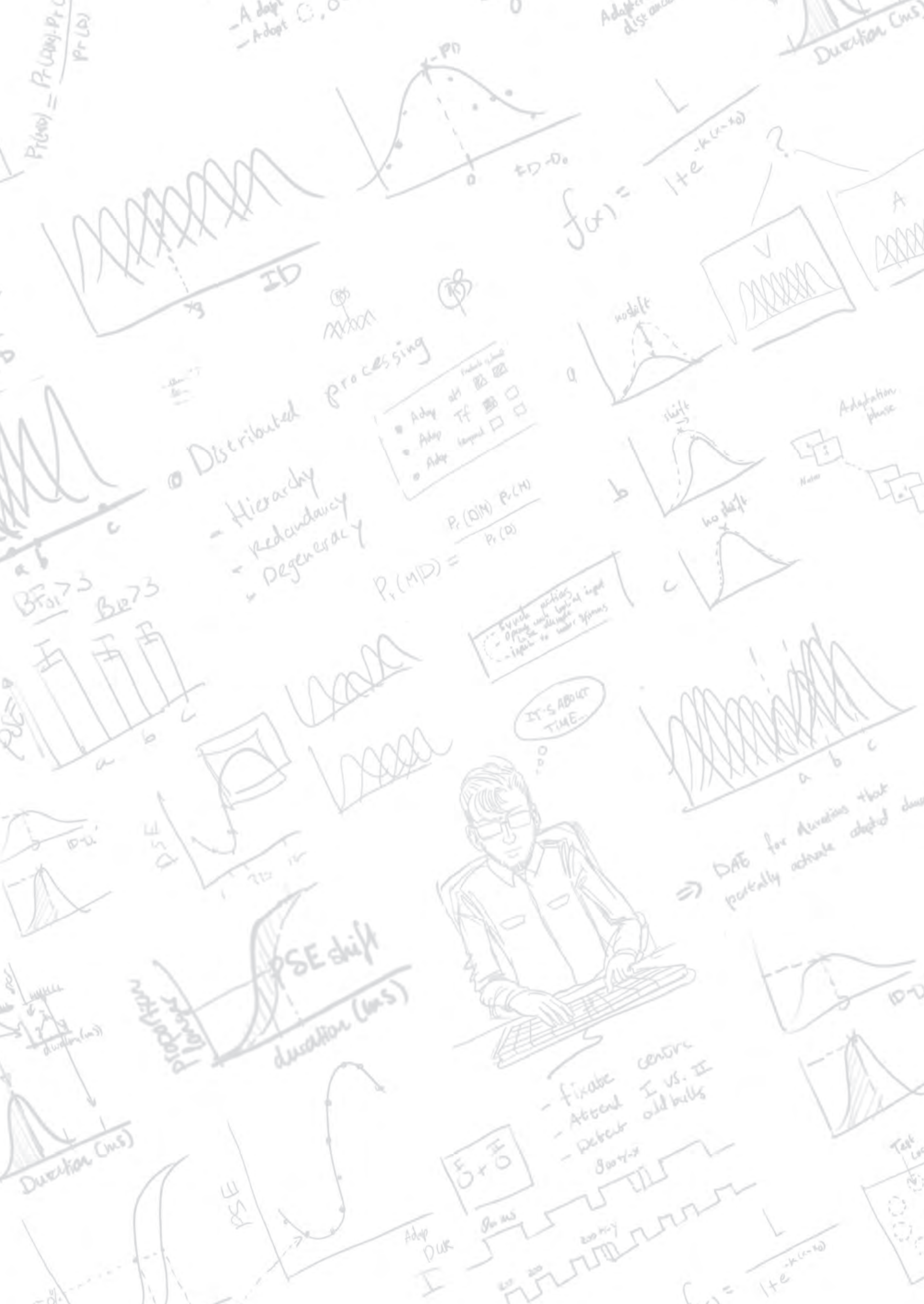
from the previous paragraph, is should be clear that there is a need for additional work aimed at integrating the duration channel model into our overall understanding of duration perception. However, I would like to emphasize that this does not mean that future research should aim to adapt and expand the duration channel model to encompass all findings in the duration perception literature. In some cases, key properties of the model or experimental findings will simply be incompatible with other findings described in the literature. For example, one of the key features of using population responses to encode a feature is that the population response is insensitive to absolute changes in stimulus saliency or intensity. This means that duration channels are simply unsuited to explain effects of stimulus intensity (Matthews, Stewart, & Wearden, 2011; Rammsayer & Verner, 2015; Xuan et al., 2007) or predictability (Pariyadath & Eagleman, 2007; Ulrich et al., 2006) on perceived duration. Similarly, studies that demonstrate that the duration encoded by duration-tuned mechanisms does not necessarily reflect the duration eventually reported by the observer (Heron et al., 2013; Chapter 4), argue that other factors influence our perception of duration independently of these duration-tuned mechanisms. In other words, it is naïve to assume that all timing behavior can or should be explained in terms of the duration channel model. Instead, it seems more fruitful to accept the idea that timing is unlikely to rely on a single mechanism, but rather consists of more distributed processes that contribute to our timing behavior. These processes could either be hierarchically structured operating by integrating output from preceding systems, or by operating separately, with different systems fulfilling similar roles under different circumstances.

Similar ideas have been put forward in the past (Bruno & Cicchini, 2016; van Wassenhove, 2009; Wiener, Matell, & Coslett, 2011), based on studies that provide empirical basis for a distributed view of duration processing. For one, a wide range of cortical and subcortical areas have been implicated in the processing of duration information (see for example: Hayashi et al., 2015; Jantzen, Steinberg, & Kelso, 2005; Meck, Penney, & Pouthas, 2008; Mello, Soares, & Paton, 2015; Merchant, Pérez, et al., 2013; Spencer & Ivry, 2013). More specifically, studies report differential activation under different tasks conditions, such as during perceptual vs. motor timing tasks (Wiener, Turkeltaub, & Coslett, 2010b) or during implicit vs. explicit duration judgement (Coull & Nobre, 2008; Wiener, Turkeltaub, & Coslett, 2010a), arguing against strong specialisation or a single neural locus. Studies on behavioral changes in duration perception also support the notion that duration processing occurs at different stages of sensory processing. For example, it has been demonstrated that adaptation to visual properties occurring in low-level visual areas can lead to compression of subsequent durations (Bruno, Ayhan, & Johnston, 2010; Johnston et al., 2006; Zhou et al., 2014). At the same time, evidence shows that the DAE results from adaptation occurring later on in the visual processing hierarchy (Heron et al., 2019; Li, Yuan, Chen, et al., 2015; Chapter 2; Chapter 3). These results show that duration perception is modulated by activity at multiple levels of visual processing. A related line of evidence for distributed processing comes from the fact that duration perception seems to rely on both unimodal and multimodal processes (Heron et al., 2012, 2013). Although not often explicitly discussed in this dissertation, our adaptation paradigm relies on the fact that adaptation using stimuli from one modality affects observers' perception of duration in the same modality, but not other modalities. This property of the duration-tuned mechanisms allows for the measurement of the DAE by comparing observers' perception of duration in the affected modality to an unaffected reference duration presented in another modality. This lack of transfer of the DAE between modalities provides direct evidence for modality specific representations of duration. At the same time, studies have shown that duration judgments made in one modality can be modulated by duration information provided in another modality (Chen & Yeh, 2009; Klink, Montijn, & van Wezel, 2011; van Wassenhove et al., 2008), arguing for the existence of a multimodal (or amodal) component to duration processing. One study combined these two behavioral manipulations and found that cross-modal modulations of duration occurred but were not reflected in the DAE following adaptation to those same stimuli (Heron et al., 2013). Similar to what we reported in chapter 4, these results argue that duration encoding does not rely solely on duration-tuned mechanisms, with multisensory interactions occurring independently of the unisensory encoding of duration.

The distributed view of duration processing raises questions about how different processes support timing behavior. One possibility is that they reflect hierarchical duration processing with each process integrating output from preceding systems. This approach leaves room for multiple types of representation of duration (as described by different models) if we assume that different representations are more suited for different purposes. For example, some duration code such as population responses might be more suited for encoding and storage, while other types of duration coding (e.g. ramping activity) could be more suited for the production of timed behavior. A hierarchal view of duration processing could also bring into perspective the behavioral findings described in the previous paragraphs. In such a case, the adaptation effects originating at different level of visual processing could indicate multiple stages of duration processing that each feed into subsequent processing steps. A similar logic can be applied to the empirical results demonstrating that the DAE does not necessarily reflect adaptation to the duration reported by the same observers (Heron, et al. 2013; chapter 4). In the case of modality specific representation of duration, the unimodal representations of duration could feed into a subsequent processing stage which uses the information to produce a multimodal or amodal representation of duration. Similarly, modulation of perceived duration as a result of increases in temporal frequency content could reflect later processing which is sensitive to multiple sources of temporal information. While these relations are currently speculative, the overall point is clear: hierarchical processing could play an important role in duration processing and could provide us with a basis to unite seemingly contradicting models and empirical results. As such, future research should critically evaluate the possibility that duration-tuned encoding of duration reflects a single processing step, extracting information from sensory input and providing output that can be used and modulated based on additional information during subsequent processing.

In contrast to the idea of hierarchical duration processing, different processes involved in duration processing might not necessarily be interconnected or hierarchically structured. Instead, it is worth considering that there is some level of degeneracy in duration processing. That is to say, multiple distinct systems might use different or even the same sources of temporal information to collectively inform timing behavior under different circumstances. These systems could reflect the different mechanisms described in different models of duration perception, as different processes might be more suited to provide duration information for certain cognitive processes or in different contexts or tasks. Given the fact that there is evidence for multiple modality-specific duration-tuned neural substrates, it is also possible that multiple duration-tuned neural substrates exist throughout the brain which can provide independent estimates of duration for different cognitive processes. Such a level of degeneracy could be considered costly from a neural standpoint; however, it also has advantages in terms of the robustness of the system. Given the fundamental importance of temporal processing for all perception and action, a distributed and degenerate network of duration processing would be beneficial to maintain timing behavior even when parts of the system are compromised (Merchant, Harrington, & Meck, 2013). In line with this idea, severe and selective distortions of timing behavior following brain damage have not been reported in the literature (Wiener et al., 2011), demonstrating that the processing of temporal information is very robust to damage to any particular part of brain.

To summarize, I propose that multiple neural processes provide complimentary and possibly degenerate sources of duration information that are used to create optimal timing behavior under different circumstances. This idea also ties in with my opening discussion on the lack of conceptual overlap between different models of duration perception. The fact that many different theories exist to describe timing behavior could be seen as a prompt to challenge ‘opposing’ theories in an attempt to falsify their description of duration processing. However, I would argue that it is more valuable to embrace the complicated nature of duration perception and to aim to integrate existing knowledge from different models. Future work should focus on evaluating the knowledge gained from different models and experimental approaches and look for ways to consolidate these into a more global framework of duration perception. Overall, the field of duration perception is evolving quickly with many new theories and experiments being published in recent years. As such, I believe that time will tell which of the different theories complement or exclude each other’s existence.


Distributed processing
- Hierarchy
- Redundancy
- Degeneracy
$P_r(M|D) = \frac{P_r(D|M)\,P_r(M)}{P_r(D)}$
$f(x) = \frac{L}{1+e^{-k(x-x_0)}}$
ID
no shift
shift
no shift
a
b
c
IT'S ABOUT TIME...
PSE shift
Proportion longer
duration (ms)
Duration (ms)
PSE
Adap DUR
- fixate centre
- Attend I vs. II
- Detect odd balls
Adaptation phase
=> DAE for durations that partially activate adapted

Appendix

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Reference list

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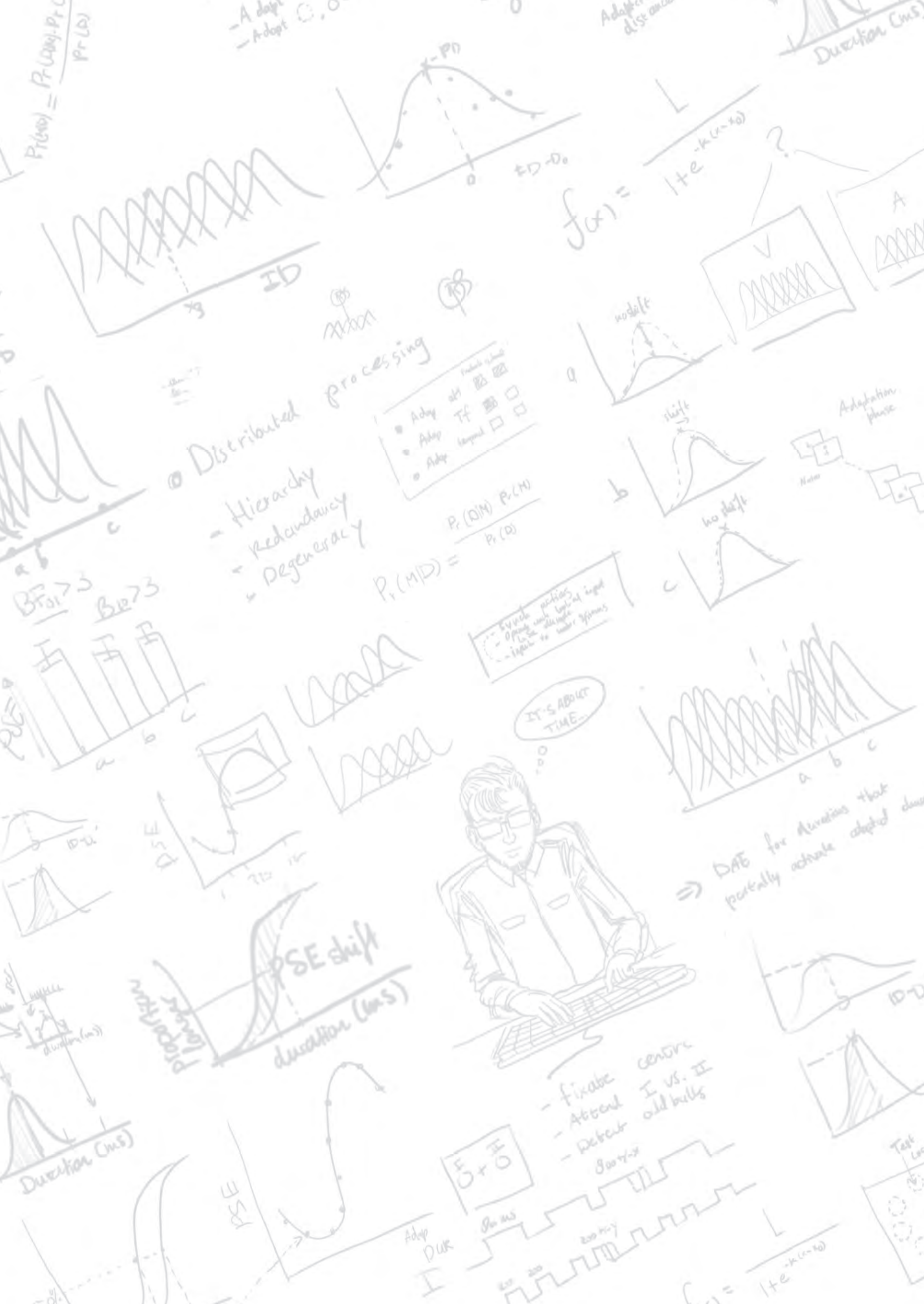
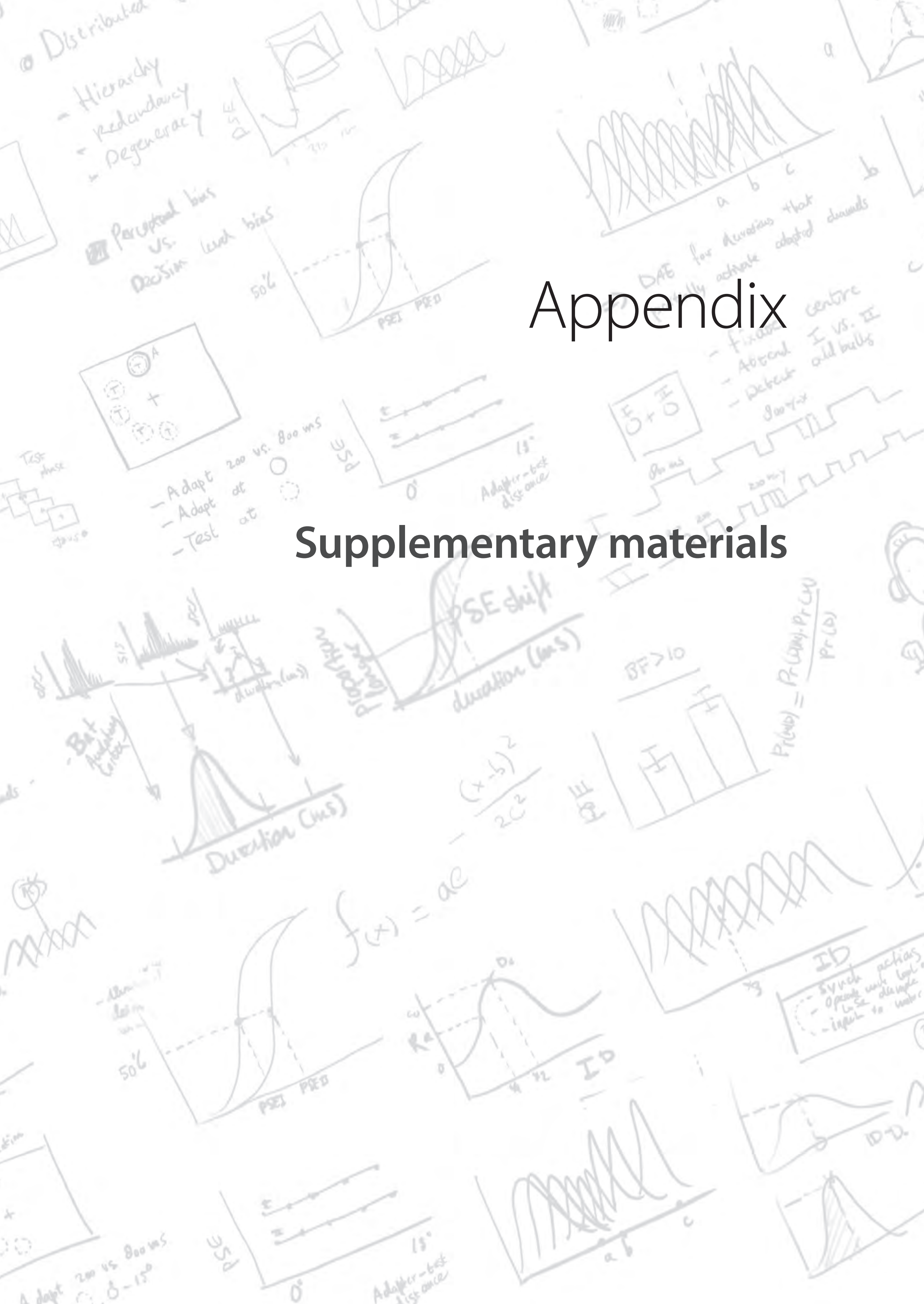

Distributed processing
- Hierarchy
- Redundancy
- Degeneracy
Pr(M|D) = Pr(D|M) Pr(M) / Pr(D)
f(x) = L / 1+e^-k(x-x0)
no shift
shift
no shift
a
b
c
BF01>3
B10>3
PSE
IT'S ABOUT TIME...
PSE shift
duration (ms)
Proportion longer
Duration (ms)
Adaptation phase
=> DAE for durations that partially activate adapted dur
- fixate centre
- Attend I vs. II
- Detect odd balls
Adap DUR
ID
ID-D0



Appendix

Supplementary materials

Chapter 2

Individual data

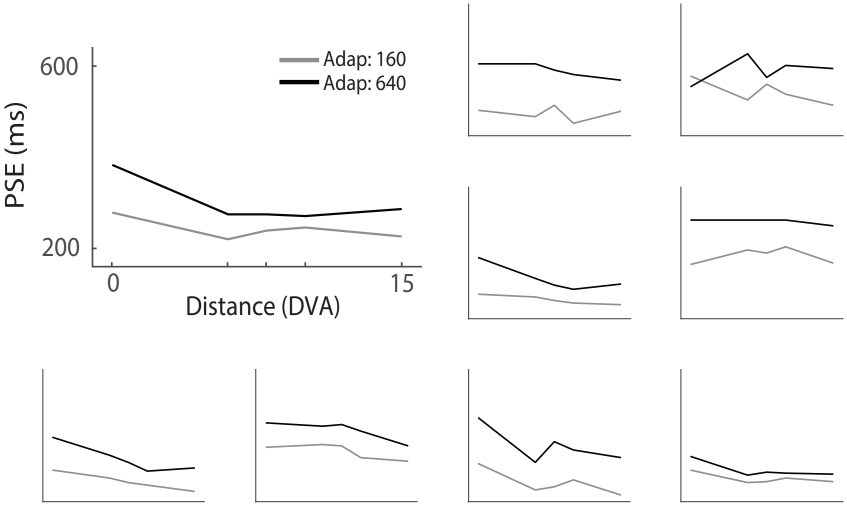


Figure S1. Individual data for Experiment 1 for each participant (N=9): Average PSEs (y-axis) as a function of distance (x-axis). A higher PSE for the 640ms Adaptation Duration (black) compared to the 160 ms Adaptation Duration (grey) reflects a Duration after-effect.

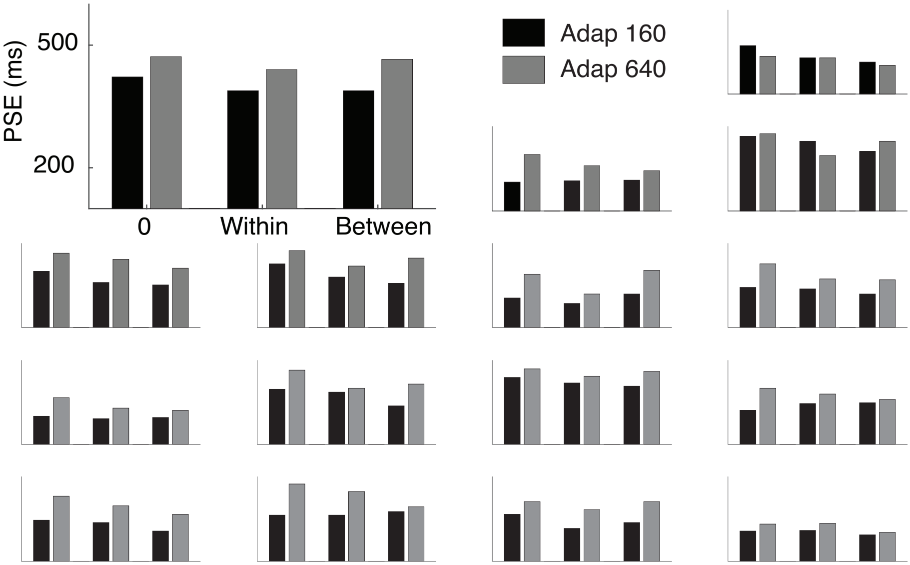


Figure S2. Individual data for Experiment 2 for each participant (N = 16): PSEs for each measured location, from left to right: same location, within hemifield, and between hemifield. A higher PSE for the 640ms Adaptation Duration (gray) compared to the 160 ms Adaptation Duration (black) reflects a Duration after-effect.

Chapter 3

Individual data

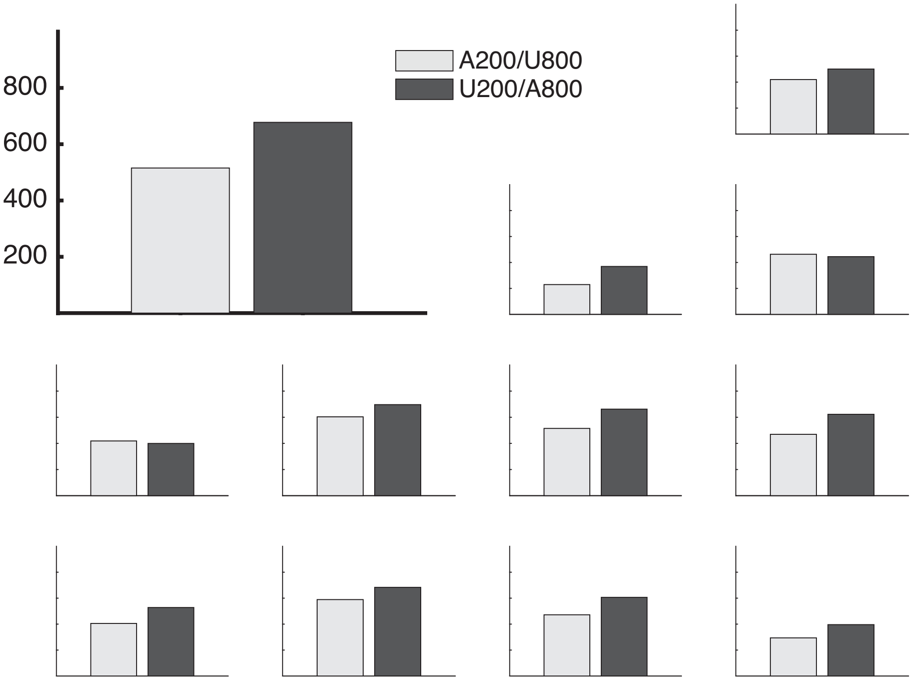


Figure S1. Individual data for Experiment 1, each graph represents median PSEs for a single participant. Higher PSEs reflect a shorter perceived duration for the test stimulus.

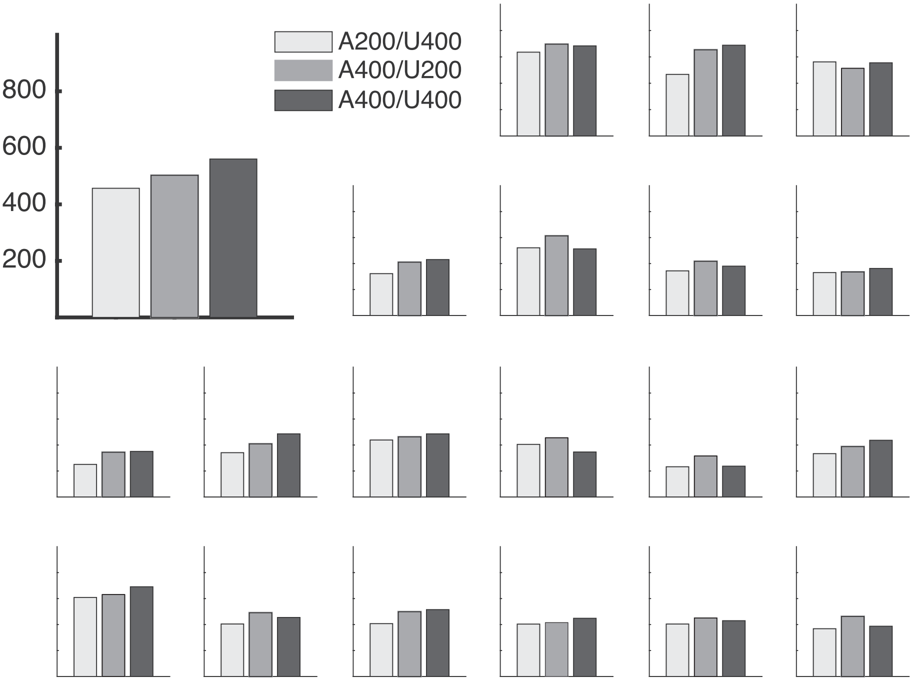
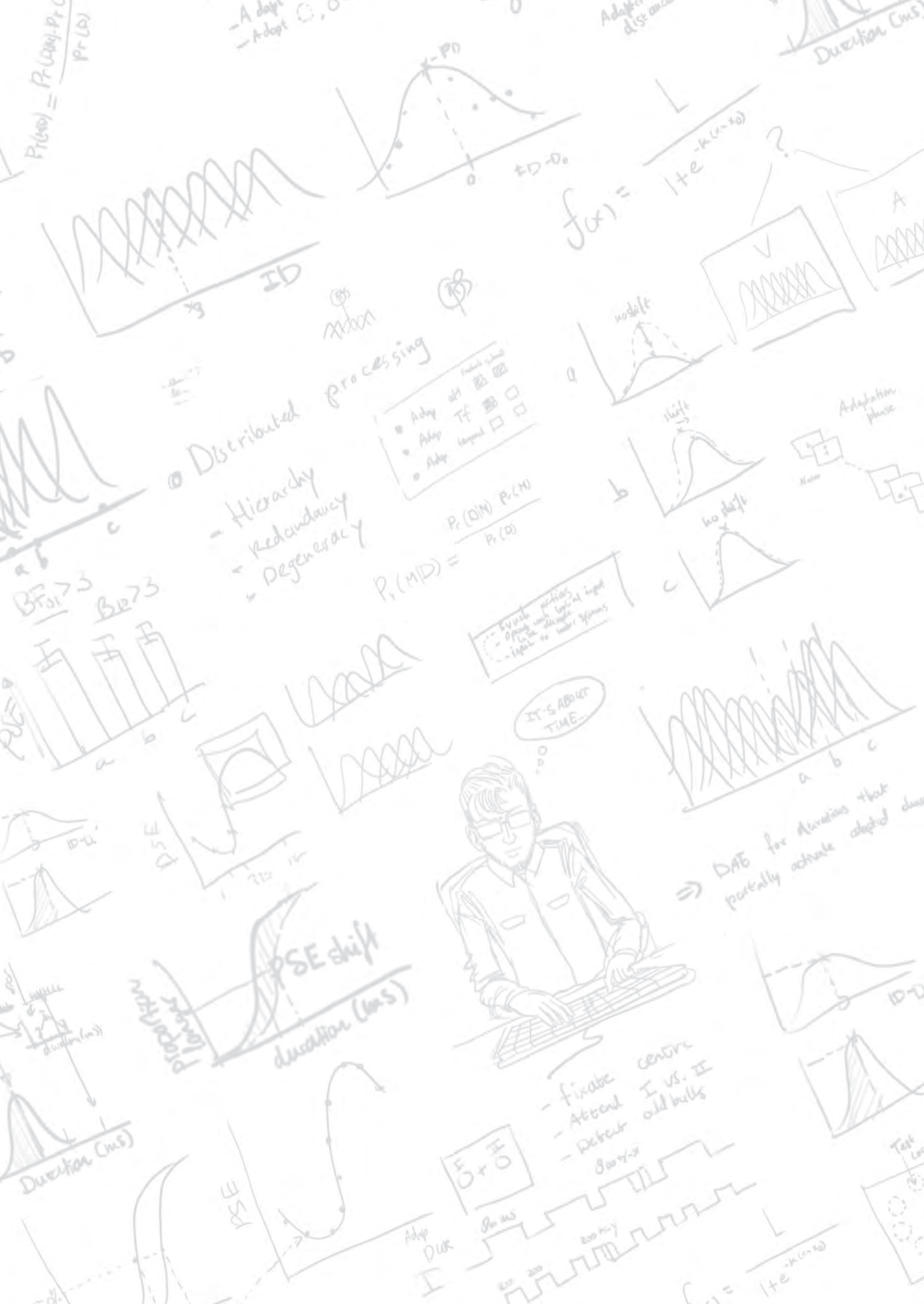


Figure S2. Individual data for Experiment 2, each image represents median PSEs for a single participant. Higher PSEs reflect a shorter perceived duration for the test stimulus.


Pr(M|D) = Pr(D|M) Pr(M) / Pr(D)
PD
ID-D0
f(x) = L / 1+e^{-k(x-x0)}
ID
x3
Distributed processing
- Hierarchy
- Redundancy
- Degeneracy
noshift
shift
no shift
a
b
c
BF01>3
B10>3
PSE
IT'S ABOUT TIME...
DAE for durations that partially activate adapted durations
PSE
PSE shift
proportion longer
duration (ms)
- fixate centre
- Attend I vs. II
- Detect odd balls
PSE
Adap DUR
Duration (ms)
Adaptation phase

Appendix

Dutch Summary

Over tijd: een studie naar de codering van tijdsduur

Ieder mens ervaart het verstrijken van de tijd. We komen uit het verleden, bevinden ons in het heden, en zijn onderweg naar de toekomst. Als onderdeel van dit proces ervaren we tijd op veel verschillende schalen. Ons leven duurt vaak vele tientallen jaren en gedurende deze jaren besteden we veel van onze tijd aan het plannen van de komende maanden, weken, dagen, uren en minuten van ons leven. Tegelijkertijd zijn we in staat om het verloop van tijd te begrijpen op tijdschalen die de grenzen van onze ervaring overschrijden. Zo hebben we bijvoorbeeld kunnen uitrekenen dat onze zon over ongeveer 10 miljard jaar zal sterven en in een zwart gat zal veranderen. Aan het andere uiterste van dit spectrum bestuderen we (sub)moleculaire processen die zich voordoen op een oneindig kleine tijdschaal. Een voorbeeld hiervan is kernsplitsing, dat nog geen 10^{-14} seconden duurt. Het is echter onze perceptie van tijd op de meest directe tijdschaal die tot onze beschikking staat, het verstrijken van (milli)seconden, dat ons bestaan regeert. Onze ervaring van tijd op die tijdschaal is namelijk cruciaal voor onze interactie met de wereld om ons heen. Het stelt ons in staat om te analyseren of gebeurtenissen tegelijkertijd of op afzonderlijke momenten plaatsvinden; om de volgorde van gebeurtenissen te beoordelen; en om temporele eigenschappen waar te nemen, zoals de duur van gebeurtenissen en de snelheid waarmee dingen over tijd veranderen. Deze kennis kunnen we gebruiken om toekomstige gebeurtenissen te voorspellen, beslissingen te nemen, en acties met de juiste timing uit te voeren. Om een beter beeld te krijgen van deze verschillende processen kunnen we kijken naar een simpele handeling zoals het vangen van een bal. Wanneer iemand een bal naar ons toe gooit komt deze met verloop van tijd dichter bij ons in de buurt. Omdat we afzonderlijke momenten in de tijd waarnemen en hun temporele volgorde kunnen beoordelen, zien we dat het moment waarop de bal dichterbij is plaatsvindt na het moment dat hij verder weg was. Hierdoor begrijpen we dat de bal naar ons toe komt en dat we moeten reageren. Vervolgens kunnen we op basis van deze ‘waarneming van opeenvolgende momenten’ bepalen met welke snelheid de bal dichterbij komt en bedenken hoe lang we nog hebben voordat de bal ons bereikt. Deze informatie kunnen we gebruiken om onze bewegingen te synchroniseren met de aankomst van de bal, om zo de bal te vangen. Dit voorbeeld geeft een passende beschrijving van de vele facetten van onze tijdsperceptie die we gebruiken om succesvol te interacteren met de wereld om ons heen.

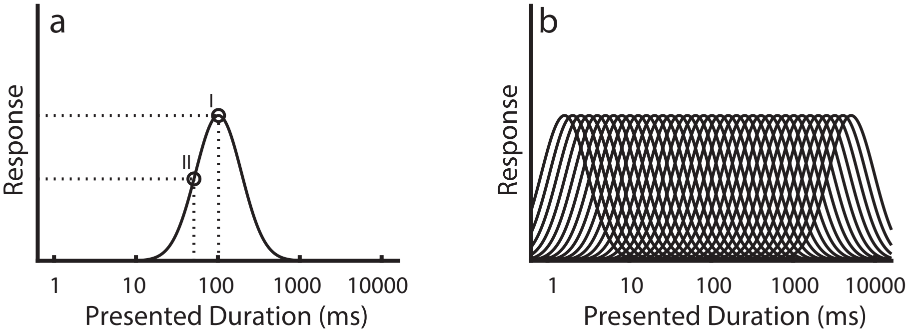
De perceptie van tijdsduur

Het is duidelijk dat het waarnemen tijd de verwerking van verschillende soorten informatie met zich meebrengt (e.g. gelijktijdigheid, volgorde, tijdsduur). Het is bijvoorbeeld mogelijk om waar te nemen dat twee dingen in een bepaalde volgorde gebeurden, zonder te weten hoeveel tijd er verstreek tussen de twee gebeurtenissen. Als zodanig kunnen verschillende soorten temporele informatie het best afzonderlijk worden beschouwd om ze goed te leren begrijpen. In het huidige proefschrift richten we ons primair op de perceptie van tijdsduur. Inzicht in de duur van een gebeurtenis, alsook de duur tussen gebeurtenissen, is de sleutel tot het begrijpen van de temporele structuur van onze omgeving. De tijd tussen onze acties en gebeurtenissen in de wereld informeert ons bijvoorbeeld of ze causaal gerelateerd zijn en helpt ons om in de toekomst op het juiste moment te handelen. Zonder tijdsduurperceptie zouden we niet kunnen begrijpen hoe ons gedrag zich verhoudt tot de resultaten die we creëren, waardoor het onmogelijk is om van onze acties te leren. Deze sleutelrol voor tijdsduurperceptie bij het sturen van ons gedrag heeft geleid tot een sterke wetenschappelijke interesse in de manier waarop we tijdsduur waarnemen.

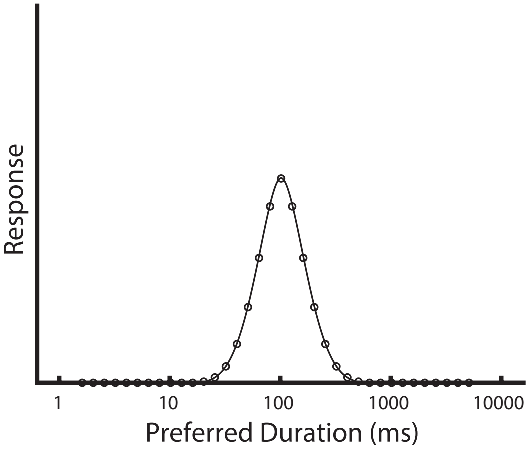
Om onze perceptie van tijdsduur te bestuderen is het interessant om te bespreken wat tijdsduur is en hoe het gemeten kan worden. Hiervoor kunnen we bijvoorbeeld kijken naar de manier waarop men denkt over duur in de natuurkunde. In deze tak van wetenschap is het verstrijken van de tijd (duur) geen fysieke eigenschap die direct gemeten kan worden. In plaats daarvan wordt duur afgeleid van veranderingen in de fysieke wereld die op verschillende momenten consistent meetbaar zijn. De SI-definitie van een seconde is bijvoorbeeld "de duur van 9 192 631 770 periodes van de straling afkomstig uit een cesium 133-atoom bij 0 graden Kelvin". Deze eigenschap van fysieke duur als afgeleide van een andere eigenschap (i.e. veranderingen binnen een atoom) wordt weerspiegeld in onze perceptie van duur. Aangezien er geen fysieke eigenschap is die direct gemeten kan worden, beschikken we niet over een zintuiglijke structuur gewijd aan de waarneming van tijdsduur. Hierin verschilt de waarneming van tijdsduur van het waarnemen van bijvoorbeeld licht. We kunnen immers zien dankzij speciale organen, de ogen, en de structuren in ons brein die de informatie vanuit onze ogen verwerken. Omdat we geen speciaal orgaan hebben om tijd te meten moet informatie over duur worden afgeleid van andere bronnen van zintuiglijke informatie die ge-encodeerd worden door de speciale zintuiglijke structuren die we wél hebben (bijvoorbeeld het visuele of het auditieve systeem). Met andere woorden, om de perceptie van tijdsduur te bestuderen moeten we kijken naar de manier waarop tijdsduurinformatie die aanwezig is in verschillende bronnen van zintuiglijke informatie wordt ge-encodeerd. Dit besef heeft ertoe geleid dat onderzoekers hebben geprobeerd om te begrijpen hoe informatie die aanwezig is in verschillende soorten sensorische input (bijvoorbeeld licht of geluid), informatie geeft over de duur van gebeurtenissen. Op deze manier kunnen we meer inzicht krijgen in de manier waarop onze hersenen tijdsduurinformatie coderen en verwerken.

Het duration channel model

Hoewel het duidelijk is dat tijdsduurinformatie een belangrijke rol speelt in ons dagelijks functioneren is ons begrip van het proces waarmee ons brein deze informatie verwerkt nog zeer beperkt. Het algemene doel van dit proefschrift was om meer inzicht te krijgen in de manier waarop we tijdsduurinformatie uit de wereld om ons heen halen en die informatie gebruiken om ons gedrag te sturen. In drie empirische hoofdstukken (hoofdstuk 2-4) bestudeerden we tijdsduurverwerking door te onderzoeken hoe tijdsduurinformatie uit visuele informatie wordt ge-encodeerd. Hierin hebben we ons gericht op het *duration channel model* (NL: tijdsduurkanalen model). Dit model stelt dat tijdsduur ge-encodeerd wordt door groepen neuronen die selectief reageren op een geprefereerde tijdsduur (Heron et al., 2012; Ivry, 1996). Wanneer een gebeurtenis wordt gepresenteerd, reageren de tijdsduur-selectieve neuronen afhankelijk van hun voorkeursduur. Een tijdsduur-selectief neuron met een voorkeursduur van 100 ms zal bijvoorbeeld sterker reageren op gebeurtenissen die 100 ms duren, maar minder activiteit vertonen bij gebeurtenissen die korter of langer duration (figuur 1a). Deze tijdsduur-selectieve neuronen zijn gegroepeerd in zogeheten tijdsduurkanalen, waarbij elk kanaal gevoelig is voor een specifieke tijdsduur (figuur 1b). Door de relatieve activering van deze tijdsduurkanalen uit te lezen, kan de duur van gebeurtenissen worden ge-encodeerd. De resulterende populatierespons biedt een expliciete weergave van de duur die vervolgens kan worden gebruikt voor verdere verwerking (figuur 2).



Figuur 1. a) De potentiele response van een enkel tijdsduur-selectief neuron als functie van de gepresenteerde tijdsduur. Het neuron reageert het sterkst wanneer de voorkeursduur wordt aangeboden (I). Bij een kortere of langere aangeboden tijdsduur verzwakt de respons (e.g. II). b) Een bank van duurkanalen elk met een verschillende voorkeursduur, hier gerepresenteerd door de piek van iedere verdeling.



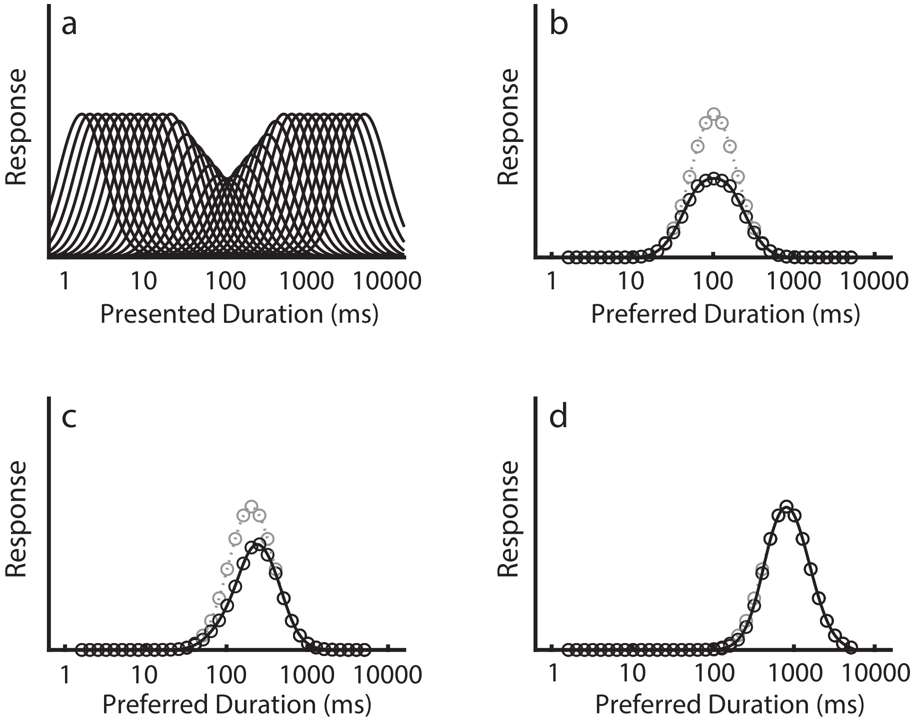
Figuur 2. De reactie van elk kanaal op een specifieke tijdsduur (100 ms) als functie van de voorkeursduur van ieder kanaal. Elke marker vertegenwoordigt de reactie van een enkel kanaal, de lijn is enkel voor visualisatiedoeleinden. De algemene vorm van de verdeling vertegenwoordigt de populatie-respons van alle kanalen bij deze specifieke tijdsduur.

Het duration channel model is een type model dat al lang geleden is geïntroduceerd binnen de psychologie. Veel van ons begrip over de codering van verschillende sensorische eigenschappen komt voort uit het toepassen van dit type model. Zo weten we bijvoorbeeld dat neuronen die selectief reageren op verschillende waardes van een eigenschap een belangrijke rol spelen in de codering van sensorische eigenschappen zoals oriëntatie (Gibson, 1937; Hubel & Wiesel, 1959), bewegingsrichting (Albright, 1984; Anstis, Verstraten, & Mather, 1998), toonhoogte (Romani, Williamson, & Kaufman, 1982), en numerositeit

(Burr & Ross, 2008; Harvey, Klein, Petridou, & Dumoulin, 2013). Het duration channel model is dus gebaseerd op een biologisch plausibel mechanisme waarvan we weten dat het gebruikt wordt om computationele uitdagingen in de hersenen op te lossen. Daarnaast biedt het duration channel model duidelijke voorspellingen voor timinggedrag en neurale reacties op duur die empirisch kunnen worden getest. Ondanks deze voordelen was er in eerste instantie weinig interesse voor de rol van tijdsduur-selectieve mechanismen in de perceptie van tijdsduur. We hebben er daarom voor gekozen om ons in deze dissertatie op het duration channel model te richten en met behulp van dit model nieuwe vragen te beantwoorden over de manier waarop ons brein informatie over tijdsduur codeert.

Empirische ondersteuning voor het duration channel model

Een bekende methode om de kanaal-gebaseerde codering van sensorische eigenschappen te bestuderen is door gebruik te maken van sensorische adaptatie. Bij sensorische adaptatie wordt door herhaaldelijk aanbieden van dezelfde informatie een deel van de neuronen die verantwoordelijk zijn voor verwerking van die informatie minder actief gemaakt. Vervolgens wordt dit verschil in activiteit gebruikt om verandering in gedrag te meten om zo conclusies te trekken over de onderliggende mechanismen. In het geval van duur voorspelt deze methode dat herhaaldelijke blootstelling aan een bepaalde tijdsduur ertoe zal leiden dat opvolgende gepresenteerde tijdsduren meer verschillend zullen lijken van de duur waaraan men eerder is blootgesteld. Dit komt doordat een deel van de kanalen minder sterk reageert (figuur 3a), waardoor de potentiele populatie respons veranderd. Omdat presentatie van de geadapteerde tijdsduur de populatie-respons niet beïnvloedt, verandert de waargenomen tijdsduur voor deze stimulus niet (figuur 3b). Voor tijdsduren die de geadapteerde kanalen gedeeltelijk activeren zal de populatieresponse wel veranderen (figuur 3c). Hierdoor zal na herhaaldelijke blootstelling aan een stimulus van bijvoorbeeld 400 ms een stimulus van 200 ms extra kort lijken te duren, en een stimulus van 800 ms juist extra lang. Wanneer de duur erg verschilt en de geadapteerde kanalen niet reageren treedt er echter geen verandering in waargenomen duur op (figuur 3d).



Figuur 3. a) Een bank met duurkanalen elk met een verschillende voorkeursduur, hier gerepresenteerd door de piek van de verdelingen. De potentiële respons van elk kanaal is veranderd als gevolg van sensorische adaptatie, met de grootste veranderingen voor kanalen waarvan de voorkeursduur overeenkwam met de tijdsduur waaraan men is geadapteerd. Elk van de andere afbeeldingen (b, c, d) toont de reacties van de kanalen op een specifieke duur als functie van de gewenste duur van de kanalen. De markers vertegenwoordigen de populatie-respons van alle kanalen op een bepaalde tijdsduur. De lijnen zijn alleen voor visualisatiedoeleinden. De grijze lijnen en bijbehorende markers tonen de populatie-responsen voor niet geadapteerd kanalen ter vergelijking. b) De populatie-respons voor een gepresenteerde tijdsduur die gelijk is aan de geadapteerde duur. De algehele populatie response is gedempt, maar de 'vorm' van de verdeling blijft hetzelfde. Hierdoor blijft de waargenomen duur ongewijzigd. c) De populatie-respons voor een gepresenteerde tijdsduur die verschilt van de tijdsduur waaraan men is geadapteerde. Omdat deze tijdsduur de aangepaste kanalen gedeeltelijk activeert, verschuift de populatie-respons weg van de tijdsduur waaraan men is geadapteerde. Als gevolg hiervan wordt de gepresenteerde duur ervaren als meer verschillend van de duur waaraan men is geadapteerd. d) De populatie-respons voor een gepresenteerde tijdsduur die sterk verschilt van de tijdsduur waaraan men is geadapteerd. Omdat deze tijdsduur de aangepaste kanalen niet activeert, verandert de populatie-respons niet. Hierdoor blijft de waargenomen duur ongewijzigd.

In lijn met bovenstaande voorspellingen hebben verschillende onderzoeken laten zien dat sensorische adaptatie optreedt en leidt tot veranderingen in de waargenomen duur van opvolgende gebeurtenissen (Heron et al., 2012; Heron, Hotchkiss, Aaen-Stockdale, Roach, & Whitaker, 2013; Li, Yuan, & Huang, 2015; Shima, Murai, Hashimoto, & Yotsumoto, 2016). In deze onderzoeken adapteerde mensen aan een specifieke visuele duur.

Om het gevolg van adaptatie te meten werd mensen vervolgens gevraagd om een cross-modale beoordeling te geven van de duur van een aantal nieuwe stimuli. Tijdens elke beoordeling vergeleken mensen de duur van een visuele teststimulus met die van een auditieve referentiestimulus. Omdat de tijdsduurverwerking van stimuli uit verschillende modaliteiten onafhankelijk gebeurt, zal de waarneming van de referentie stimulus niet beïnvloed worden door de adaptatie. Hierdoor is het mogelijk om veranderingen in de waarneming van de teststimuli te meten tegenover een 'vast' referentie punt. Zo kunnen de gevolgen van adaptatie gemeten worden en de gemaakte voorspellingen worden getest. Op deze manier werd in bovenstaande studies aangetoond dat adaptatie inderdaad leidt tot de verwachte perceptuele verandering: na adaptatie aan een specifieke tijdsduur lijken andere tijdsduren meer verschillende te zijn van de geadapteerde tijdsduur. Daarnaast hebben Heron en collega's (2012) adaptatie gemeten voor een breed scala aan duren (40 - 2560 ms) en laten zien dat dit gevolg van adaptatie alleen plaatsvindt wanneer de geadapteerde duur dicht bij de geteste duur lag, maar verdwijnt wanneer het verschil tussen de adaptatieduur en de testduur te groot werd. Dit effect van adaptatie op de waarneming van tijdsduur wordt het tijdsduur na-effect, ofwel het *duration after-effect* (DAE) genoemd. Het optreden van het DAE in bovenstaande studies levert een belangrijke bron van bewijs voor het voorstel dat tijdsduur-selectieve kanalen ten grondslag liggen aan de codering van tijdsduur.

Naast de hierboven beschreven adaptatiestudies zijn er verschillende andere studies die het idee van tijdsduur-selectieve codering van duur ondersteunen. Zo hebben studies laten zien dat mensen na training beter worden in het onderscheiden van tijdsduur, maar alleen voor de duren waarop men is getraind (Bueti & Buonomano, 2014; Karmarkar & Buonomano, 2003; Nagarajan, Blake, Wright, Byl, & Merzenich, 1998; Wright, Buonomano, Mahncke, & Merzenich, 1997). Deze trainingsresultaten zijn te verklaren als men aanneemt dat de training verandering heeft teweeg gebracht in de tijdsduurkanalen die betrokken waren bij het encoderen van de getrainde duur (Bueti & Buonomano, 2014). Naast deze gedragsstudies zijn er ook neurofysiologische studies bij dieren en fMRI studies bij mensen die bewijs leveren voor tijdsduur-selectieve codering van duur. Zo hebben verschillende dierenstudies laten zien dat er individuele neuronen in het brein zijn die tijdsduur-selectieve responsen vertonen (Duysens, Schaafsma, & Orban, 1996;

Ehrlich, Casseday, & Covey, 1997; He, Hashikawa, Ojima, & Kinouchi, 1997; Merchant, Pérez, Zarco, & Gámez, 2013; Mita, Mushiake, Shima, Matsuzaka, & Tanji, 2009; Wu & Jen, 2008). Recentelijk zijn er ook een aantal studies gepubliceerd die door middel van fMRI laten zien dat tijdsduur-selectieve responsen voorkom in verschillende hersengebieden in het menselijk brein (Hayashi et al., 2015; Hayashi, van der Zwaag, Bueti, & Kanai, 2018; Protopapa et al., 2018). Zo heeft een recente studie van Protopapa et al. (2018) laten zien dat tijdsduur-selectieve activiteit optreedt in de supplementaire motorische schors en de obulus parietalis inferior. Bovendien vertoonde deze tijdsduur-selectieve neuronen een chronotope organisatie waarbij groepen neuronen die gevoelig zijn voor vergelijkbaar tijsduren als een gradiënt over de oppervlakte van het brein verspreid liggen. Dit type ruimtelijke organisatie wordt ook gevonden bij andere stimuluseigenschappen die worden ge-encodeerd door eigenschap-selectieve neurale systemen, zoals bijvoorbeeld de kolomorganisatie van oriëntatie-selectieve neuronen in visueel gebeid V1, (Yacoub, Harel en Ugurbil, 2008) en de topografische ordening van numerositeit-selectieve neuronen, Harvey et al., 2013).

Het DAE gebruiken om duur codering te bestuderen

De studies die ik tot nu toe heb beschreven, bieden convergente bewijzen voor het idee dat tijdsduur-selectieve mechanismen een rol spelen bij het coderen van duur. Ons begrip van de exacte aard van deze tijdsduur-selectieve mechanismen en hun werking is echter nog beperkt. Ten eerste zijn veel van de veronderstellingen van het duration channel model gebaseerd op bestaande kennis over de verwerking van niet-temporele sensorische eigenschappen zoals oriëntatie en spatiale frequentie. Het is echter niet duidelijk in hoeverre tijdsduur-selectieve neurale structuren de structurele en functionele eigenschappen van deze vergelijkbare processen zullen weerspiegelen. Veel van de uitvoerig bestudeerde visuele functies, zoals oriëntatie, worden bijvoorbeeld ge-encodeerd door vroege visuele gebieden die een hoog niveau van structurele en functionele organisatie vertonen. Zo zijn cellen in de cortex op het niveau van visueel gebied V1 bijvoorbeeld georganiseerd in kolommen, waarbij iedere kolom gevoelig is voor een specifieke oriëntatie. De codering van numerositeit gebeurt ook op basis van selectiviteit voor specifieke aantallen, maar de hersengebieden die hiervoor verantwoordelijk zijn meer verspreid door het brein (Harvey & Dumoulin, 2016). Gezien deze verschillen kunnen we niet met zekerheid zeggen welke delen van de hersenen verantwoordelijk zullen zijn voor de codering van tijdsduur. Daarnaast is het niet bekend welke visuele informatie (of neurale input) door de hersenen wordt gebruikt om tijdsduurinformatie te extraheren. Nader onderzoek is noodzakelijk om deze basiseigenschappen van het duration channel model te begrijpen.

Momenteel is het ook onduidelijk hoe het duration channel model en empirische bevindingen zoals het DAE zich verhouden tot andere bevindingen in de literatuur over de tijdsduurperceptie. Zo is er veel werk verricht naar de perceptie van tijd dat niet gemakkelijk kan worden verklaard door het duration channel model in zijn huidige vorm. Dit roept vragen op over de rol van tijdsduur-selectieve mechanismen in ons algehele vermogen om tijdsduurinformatie te coderen, op te slaan en te gebruiken. Om deze vragen te kunnen beantwoorden, is een dieper begrip nodig van de neurale mechanismen die ten grondslag liggen aan de kanaal-gebaseerde codering van tijdsduur.

In dit proefschrift hebben we de techniek van sensorische adaptatie gebruikt om verschillende vragen te beantwoorden over tijdsduur-selectieve mechanismen en de rol die ze spelen in tijdsduurcodering. Het optreden van het DAE weerspiegelt veranderingen in het activiteitprofiel van de neurale structuren die verantwoordelijk zijn voor duurcodering. Als zodanig kunnen we het optreden van het DAE gebruiken als een meting van de activering die plaatsvindt in tijdsduur-selectieve neurale structuren tijdens adaptatie. Door de experimentele omstandigheden tijdens adaptatie te manipuleren, kunnen we het effect van deze manipulatie op het duurcoderingsproces meten. Dit stelt ons in staat om het coderingsproces van de duur te onderzoeken en conclusies te trekken over de onderliggende neurale structuren en hun (functionele) eigenschappen. Op deze manier biedt het DAE een uniek hulpmiddel waarmee we de ruimtelijke en temporele eigenschappen van duurcodering kunnen bestuderen, evenals de extractie van tijdsduurinformatie uit verschillende bronnen van sensorische informatie onder verschillende gedragsomstandigheden.

Hoofdstuk 2

In hoofdstuk 2 hebben we de ruimtelijke selectiviteit van het DAE bestudeerd om meer inzicht te krijgen in de relatieve positie van tijdsduur-selectieve mechanismen binnen de visuele verwerkingshiërarchie. Hierbij wilden we beoordelen of tijdsduur-selectieve mechanismen zich in vroege visuele gebieden bevinden. Om dit te bereiken hebben we het DAE gemeten in verschillende situaties waarbij de afstand tussen de adaptatiestimulus en de teststimulus werd gevarieerd tussen de 0 en 15° (visuele graden). Uit eerder onderzoek weten we dat de visuele afstand waarover sensorische informatie wordt geïntegreerd toeneemt naarmate de informatie hoger in de visuele verwerkingshiërarchie beland (Smith, Singh, Williams, & Greenlee, 2001). Dit is het gevolg van een toename in de grootte van de receptieve velden – het deel van de visuele ruimte waarvan het neuron informatie binnenkrijgt – van individuele neuronen in deze verschillende corticale gebieden. De grootte van de receptieve velden van individuele neuronen neemt namelijk sterk toe naarmate deze zich hoger in de visuele verwerkingshiërarchie bevinden (Amano, Wandell, & et al., 2009; Dumoulin & Wandell, 2008; Harvey & Dumoulin, 2011; Smith et al., 2001). Als gevolg van deze eigenschap van het visuele systeem zijn na-effecten die optreden als gevolg van adaptatie in vroege visuele gebieden beperkt tot relatief kleine delen van de visuele ruimte. Na-effecten die optreden als gevolg van adaptatie in latere visuele gebieden treden juist op over grote delen van de visuele ruimte. Op basis van deze kennis kunnen we de volgende hypothese opstellen: Als de codering van tijdsduur vroeg in de visuele verwerkingshiërarchie plaatsvindt zou het DAE beperkt moeten blijven tot enkele visuele graden vanaf de geadapteerde locatie. Echter, als de codering van duur later in de visuele verwerkingshiërarchie plaatsvindt, zal het DAE relatief constant blijven over de gehele visuele ruimte waarin we testen. In twee experimenten vonden we duidelijk bewijs voor een DAE op alle gemeten afstanden (0-15 °), zonder bewijs voor een afname van de omvang van het DAE als functie van de afstand. Deze resultaten tonen aan dat het DAE niet het gevolg is van adaptatie in vroege delen van de visuele verwerkingshiërarchie. We concludeerden dan ook dat tijdsduurinformatie waarschijnlijk een complexe stimulus eigenschap is die pas later in de visuele verwerkingshiërarchie wordt ge-encodeerd.

Hoofdstuk 3

In hoofdstuk 3 gebruikten we duuradaptatie om de rol van aandacht in de selectieve codering van tijdsduur te onderzoeken. Hierbij waren we met name geïnteresseerd in situaties waarin meerdere bronnen van tijdsduurinformatie aanwezig zijn. Veel onderzoekers hebben gepostuleerd dat er een belangrijke rol is voor aandacht in het coderen van relevante tijdsinformatie (Gibbon, Church, & Meck, 1984; Meck, 1984; Pariyadath & Eagleman, 2007; van Rijn, Gu, & Meck, 2014; Zakay & Block, 1997). Dit voorstel sluit aan bij onderzoeken die aantonen dat aandacht een belangrijke rol speelt bij de selectieve codering van relevante versus niet-relevante stimulusinformatie door middel van modulatie van de mate waarin visuele informatie door neuronen wordt ge-encodeerd (Alais & Blake, 1999; James, 1890; Lankheet & Verstraten, 1995; Moran & Desimone, 1985; Murray & Wojciulik, 2004; Spivey & Spirn, 2000; Treue & Martínez Trujillo, 1999).

Om de rol van aandacht bij het verzamelen van tijdsduurinformatie te evalueren, hebben we ons adaptatieparadigma aangepast om de presentatie van tijdsduurinformatie uit meerdere bronnen mogelijk te maken. Deelnemers werden gepresenteerd met twee gelijktijdig stromen van adaptatiestimuli met verschillende tijdsduren. Vervolgens werden zij gevraagd om in een van deze stromen een afwijkende tijdduur te detecteren. Als gevolg hiervan ging meer van de aandacht van de deelnemers richting een van de twee stromen. Dit stelde ons in staat om een vergelijking te maken tussen het DAE wanneer men lette op de ene of de andere bron van tijdsduurinformatie. Aangezien het DAE een gevolg is van selectieve adaptatie van de tijdsduur-selectieve kanalen (Heron et al., 2012), kan modulatie van het DAE worden geïnterpreteerd als een verandering in de sterkte van de codering van de gepresenteerde tijdsduurinformatie. Als aandacht de mate waarin tijdsduurinformatie wordt ge-encodeerd moduleert, zou het concentreren op één bron van tijdsduurinformatie moeten leiden tot een sterker na-effect voor die bron in vergelijking met de genegeerde bronnen van tijdsduurinformatie. De relatieve bijdrage van de twee stromen van tijdsduurinformatie op het DAE zou dus moeten verschuiven richting de duur waarop men de aandacht vestigde. In onze experimenten zagen we dat het DAE het gevolg was van adaptatie aan tijdsduurinformatie waarop men de aandacht richtte, en niet van adaptie aan de informatie waar geen aandacht aan werd besteed. In het tweede experiment hebben we een extra 'referentie' conditie toegevoegd waarin geen DAE optrad. Hierdoor konden we de relatieve bijdrage van geattendeerde versus ongeattendeerde duurinformatie meten. Onze resultaten toonden aan dat de ongeattendeerde duur niet bijdroeg aan het gemeten DAE. Samen tonen deze resultaten aan dat aandacht een cruciale rol speelt bij de selectieve codering van tijdsduur: duur waar men aandacht aan besteed wordt ge-encodeerd terwijl duur waar men geen aandacht aan besteed niet of nauwelijks verwerkt wordt. We concludeerden daarom dat visuele aandacht ten grondslag ligt aan de selectie van relevante tijdsinformatie wanneer er meerdere bronnen van tijdsinformatie aanwezig zijn.

De sterke rol van aandacht in de codering van duur sluit aan bij onze eerdere bevinding dat tijdsduur relatief laat in de visuele verwerkingshiërarchie wordt ge-encodeerd (hoofdstuk 2). Eerder onderzoek heeft aangetoond dat de mate waarin aandacht de neuronale reacties op een bepaald stimuluskenmerk kan beïnvloeden, afhangt van de complexiteit van dat kenmerk en de positie van de verwerking in de visuele verwerkingshiërarchie (Suzuki, 2001). Dit komt doordat de response van individuele cellen op informatie waar geen aandacht aan besteed wordt steeds meer afneemt naar mate de positie in de visuele verwerkingshiërarchie toeneemt. Zo neemt de reactie op on-geattendeerde informatie af tot ~ 30% in het vroege visuele gebied V2, en neemt deze verder af tot 0% in cellen in het gebied IT (Chelazzi, Duncan, Miller, & Desimone, 1998; Reynolds, Chelazzi, & Desimone, 1999). Dit komt overeen met het feit dat we geen relatieve bijdrage aan het DAE vonden voor de tijdsduurinformatie waaraan geen aandacht aan besteed werd. De sterke aandachtmodulatie die we hier vinden ondersteunt dus het idee dat tijdsduur een complex kenmerk is dat ge-encodeerd wordt door mechanismen die zich op hogere niveaus van de verwerkingshiërarchie bevinden.

Hoofdstuk 4

In hoofdstuk 4 hebben we onderzocht wat de aard is van het signaal waar de tijds-selectieve kanalen op reageren. Er wordt vaak gesteld dat de codering van duur door tijdsduur-selectieve mechanismen gebeurt op basis van de tijd tussen het begin en het einde van een gebeurtenis (Heron et al., 2012). Dit idee klinkt logisch: als je weet wanneer iets begint en wanneer het eindigt weet je ook hoe lang het duurt. Toch zijn er studies die aantonen dat de waargenomen duur van een gebeurtenis kan veranderen, zonder dat het waargenomen begin en/of eind van dezelfde gebeurtenis verandert (Kaneko & Murakami, 2009). Deze dissociatie tussen de waargenomen signaallengte (begin tot einde) en de waargenomen duur lijkt in schril contrast te staan met het idee dat tijdsduur-selectieve kanalen uitsluitend gebruik maken van de lengte van het zintuiglijke signaal. Om deze dissociatie te adresseren hebben we deelnemers geadapteerd aan een illusie-inducerende stimulus die bestond uit een roterend patroon. Dit type stimulus zorgt voor een toename van de waargenomen duur, zonder dat dit invloed heeft op het waargenomen begin en eind van de stimulus (Kaneko & Murakami, 2009). Ook adapteerde we de deelnemers aan twee 'controle patronen'. Een statisch patroon waarvan de duur gelijk was aan de illusie-inducerende stimulus (de begin-einde gematchte stimulus) en aan een statisch patroon dat even lang duurde als de door de proefpersoon waargenomen duur van de illusie-inducerende stimulus (de perceptueel gematchte stimulus). Dit stelde ons in staat om het DAE na adaptatie aan de illusie-inducerende stimulus te vergelijken met twee 'controle' condities. Als deelnemers adapteren aan de signaalduur van een gebeurtenis, verwachten we dat het DAE voor de illusie-inducerende stimulus vergelijkbaar is met het DAE voor de begin-einde gematchte stimulus. Als deelnemers adapteren aan de waargenomen duur van een gebeurtenis, dan verwachten we dat het DAE voor de illusie-inducerende stimulus juist vergelijkbaar is met het DAE voor de perceptueel gematchte stimulus. We vonden dat het DAE voor de illusie-inducerende stimulus niet verschilde van het DAE voor de begin-einde gematchte stimuli, maar wel verschilde van het DAE voor de perceptueel gematchte stimuli. Met andere woorden: deelnemers adapteerde aan de signaalduur en niet aan een duur die overeenkomt met de waargenomen duur van de illusie-inducerende stimulus. We concludeerden dat kanaal-gebaseerde duurcodering gebaseerd is op de signaallengte van een gebeurtenis en niet noodzakelijkerwijs overeenkomt met de waargenomen duur van diezelfde gebeurtenis.

De resultaten van hoofdstuk 4 demonsteren een belangrijke rol voor informatie over het begin en het einde van een gebeurtenis in tijdsduurcodering. Deze bevinding sluit aan bij eerder werk waarin werd aangetoond dat capaciteitslimieten in de tijdsduurverwerking sterk gekoppeld zijn aan de mate waarmee het begin en einde van de verschillende duurstimuli overlappen (van Rijn & Taatgen, 2008). Het vermogen om informatie over de duur van meerdere gebeurtenissen effectief te coderen lijkt dus te berusten op de verwerking van het begin en het einde van de gebeurtenissen. Interessant is ook dat dit suggereert dat het niet noodzakelijk is om het hele interval te verwerken en dat attenderen aan het begin en het einde van de gebeurtenis voldoende kan zijn om de duur ervan te coderen. Samen met de resultaten van hoofdstuk 3 onderstrepen deze resultaten het idee dat duurcodering een proces is dat afhankelijk is van de selectie van relevante begin- en einde- informatie om de duur te coderen.

De perceptie van verandering

Een andere belangrijke bron van tijdsinformatie is de snelheid waarmee de wereld om ons heen verandert. Verandering informeert ons over het feit dat de tijd verstrijkt en zorgt voor herkenbare momenten in de tijd die ons in staat stellen de volgorde en duur van gebeurtenissen te analyseren. Aangezien er waarschijnlijk meer tijd passeert naarmate er meer dingen veranderen, kan verandering ons ook informeren over de duur van gebeurtenissen. Dit heeft geleid tot interesse in de rol van informatie over verandering (ook wel temporele frequentie) in de perceptie van tijdsduur (Brown, 1995; Kanai, Paffen, Hogendoorn, & Verstraten, 2006; Poynter, 1989). Wetenschappelijke studies hebben dan ook aangetoond dat gebeurtenissen met een hogere temporele frequentie leiden tot een langere waargenomen duur (Brown, 1995; Herbst, Javadi, van der Meer, & Busch, 2013; Kanai et al., 2006; Linares & Gorea, 2015). Ook hebben Rosenboom en collega's onlangs aangetoond dat een model dat uitsluitend gebaseerd is op de veranderingen in een visuele scène kan worden gebruikt om een systeem te creëren dat het verstrijken van tijd in deze omgeving betrouwbaar kan coderen (Roseboom et al., 2017). Samen onderstrepen deze bevindingen het belang van het begrijpen van de verwerking van temporele frequentie (de mate van verandering) in onze zoektocht om de verwerking van tijdsinformatie in het algemeen beter te begrijpen.

In hoofdstuk 5 gebruikte we de interactie tussen temporele frequentie en tijdsduur als een manier om de representatie van temporele frequentie informatie te bestuderen in situaties waarin de bron van informatie tijdelijk niet zichtbaar is. Het is bekend dat mensen de visuele kenmerken van objecten representeren wanneer ze tijdelijk niet zichtbaar zijn door occlusie. Deze representaties stellen ons in staat om gebeurtenissen die zich buiten voordoen tijdens occlusie te extrapoleren en snel objecten te identificeren wanneer ze weer tevoorschijn komen. Eerder werk heeft zich vooral gericht op de representatie van statische eigenschappen van geoccludeerde objecten. In veel situaties veranderen de visuele kenmerken juist als functie van de tijd. Het weergeven van deze veranderingen, en de snelheid waarmee ze zich voordoen, kan extra voordelen bieden voor de extrapolatie en identificatie van geoccludeerde objecten. In hoofdstuk 5 hebben we onderzocht of informatie over de snelheid waarmee visuele informatie verandert ook wordt gerepresenteerd tijdens occlusie.

Om deze vraag te beantwoorden gebruikten we de *Temporal Frequency Induced Time Dilation* (nl: temporele frequentie geïnduceerde tijdsverruiming) illusie waarbij de waargenomen duur van een gebeurtenis toeneemt als functie van de temporele frequentie-inhoud ervan (Kanai et al., 2006). Door deze illusie te combineren met een situatie waarin het object wordt geoccludeerd, kunnen we het effect van de temporele frequentie-inhoud op de waargenomen duur van de geoccludeerde stimulus onderzoeken. Als de temporele frequentie-inhoud van de illusie-veroorzakende stimulus tijdens occlusie wordt gerepresenteerd, zou dit de waargenomen duur van de gebeurtenis nog steeds moeten beïnvloeden, zelfs wanneer het object niet langer zichtbaar is. In experiment één toonden we aan dat de temporele frequentie-inhoud van een gebeurtenis de waargenomen duur van deze gebeurtenis beïnvloedt, zowel wanneer deze zichtbaar blijft als wanneer deze tijdelijk wordt geoccludeerd. In een tweede experiment toonde we aan dat de modulatie van de waargenomen duur van geoccludeerde gebeurtenissen ook beïnvloed wordt door de verwachte temporele frequentie-inhoud van het object tijdens occlusie. Samen tonen deze resultaten aan dat de temporale frequentie-inhoud van een object tijdens occlusie wordt gerepresenteerd. We concludeerden dat de representaties van geoccludeerde objecten een breed scala aan kenmerken bevatten die afgeleid zijn uit de periode dat het object nog zichtbaar was. Hieronder valt informatie over zowel de statische als dynamische eigenschappen van het object.

Conclusie

Het onderzoek dat in dit proefschrift wordt gepresenteerd had als doel om ons begrip van de codering en het onderhoud van temporele informatie te vergroten. Hierin hebben we ons met name gericht op de rol van tijdsduur-selectieve mechanismen in de codering van tijdsduur. We hebben een aantal assumpties van het duration channel model getest, alsook de algemene assumpties die aanwezig zijn in de literatuur over de waarneming van tijdsduur. We hebben aangetoond dat tijdsduur-selectieve mechanismen: zich relatief laat in de visuele verwerkingshiërarchie bevinden (hoofdstuk 2), afhankelijk zijn van aandacht voor het effectief selecteren van tijdsduurinformatie wanneer er meerdere bronnen van tijdsduurinformatie aanwezig zijn (hoofdstuk 3), en de duur coderen op basis van de lengte van het sensorische signaal (hoofdstuk 4). Hieruit concluderen we dat duur een complexe stimulus is, die wordt ge-encodeerd via een inspannend proces waarbij aandacht wordt besteed aan het selecteren van relevante informatie voor het coderen van de duur. Samen tonen deze studies de waarde aan van het gebruik van het duration channel model en de methode van sensorische adaptatie, als leidend kader voor het bestuderen van de codering van duur.

Appendix

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Mijn ouders en zusje. **Joke en Ed van Balen**. Jullie zijn de veilige basis van waaruit ik alles in het leven heb kunnen ondernemen. Jullie waren al trots toen ik de basisschool af had gemaakt, dus alles daarna was mooi meegenomen. Toch is het fijn om te weten dat jullie altijd trots op me zullen zijn en altijd van me zullen houden. Dikke knuffel. **Bram Maarseveen.** Pa, jij hebt me geleerd om altijd nieuwe dingen te blijven proberen, om mijn eigen kunnen te benutten, en om me niet te veel van anderen aan te trekken. Naarmate ik ouder word denk ik steeds vaker aan deze lessen terug. I love you! **Eva Maarseveen**, lief zussie. Samen met papa ben jij mijn gekke tweede gezin waar ik heel veel van houd maar gelukkig niet mee in één huis hoefde te wonen. Ik hoop dat Sine en James veel met elkaar kunnen spelen de komende jaren. I love you ook! **Han en Lettie & Borek en Kim,** na al die jaren zijn jullie net zo goed familie als mijn eigen ouders en zus. Bedankt voor alle steun en gezelligheid. **Oma Co**, het voelde misschien als 90 jaar wachten maar het is me gelukt. Ik ben blij dat u erbij kon zijn om mij te zien promoveren. **Opa & Oma Maarseveen, Cock & Cees,** bedankt voor de liefde en het begrip.

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Katinka. Soms bedanken mensen hier ook al hun exen, maar aangezien dat niet van toepassing is heb ik besloten om een paar Katinka's van verschillende jaargangen te bedanken.

Middelbare school Katinka. Mijn eerste echte liefde. Toen mij verteld werd dat ik niet van 4-havo naar 5-vwo mocht gaan, nam jij daar geen genoegen mee. Je hebt me achter je aangesleept langs alle leraren die aan mij twijfelden en net zo lang op ze ingepraat tot je ze allemaal had overtuigd. Jouw vertrouwen in mij heeft ervoor gezorgd dat ik altijd probeer door te zetten tot het einde.

Studententijd Katinka. Jij netjes aan het studeren, en ik op de achtergrond aan het lanterfanten. Toch was jouw harde werk altijd een inspiratie om te zorgen dat ik ook door bleef werken aan wat ik wilde bereiken.

PhD-tijd Katinka. Deze Katinka heeft het niet altijd makkelijk gehad. Ik was altijd maar bezig met mijn PhD en als het niet goed ging nam ik dat allemaal mee naar huis. Naast het afronden van je eigen PhD heb je veel energie gestoken om mij positief te houden en me te motiveren om het allemaal af te ronden. Ik heb veel van je geleerd over loslaten en het balanceren van werk en privé en heb veel van deze jaren geleerd.

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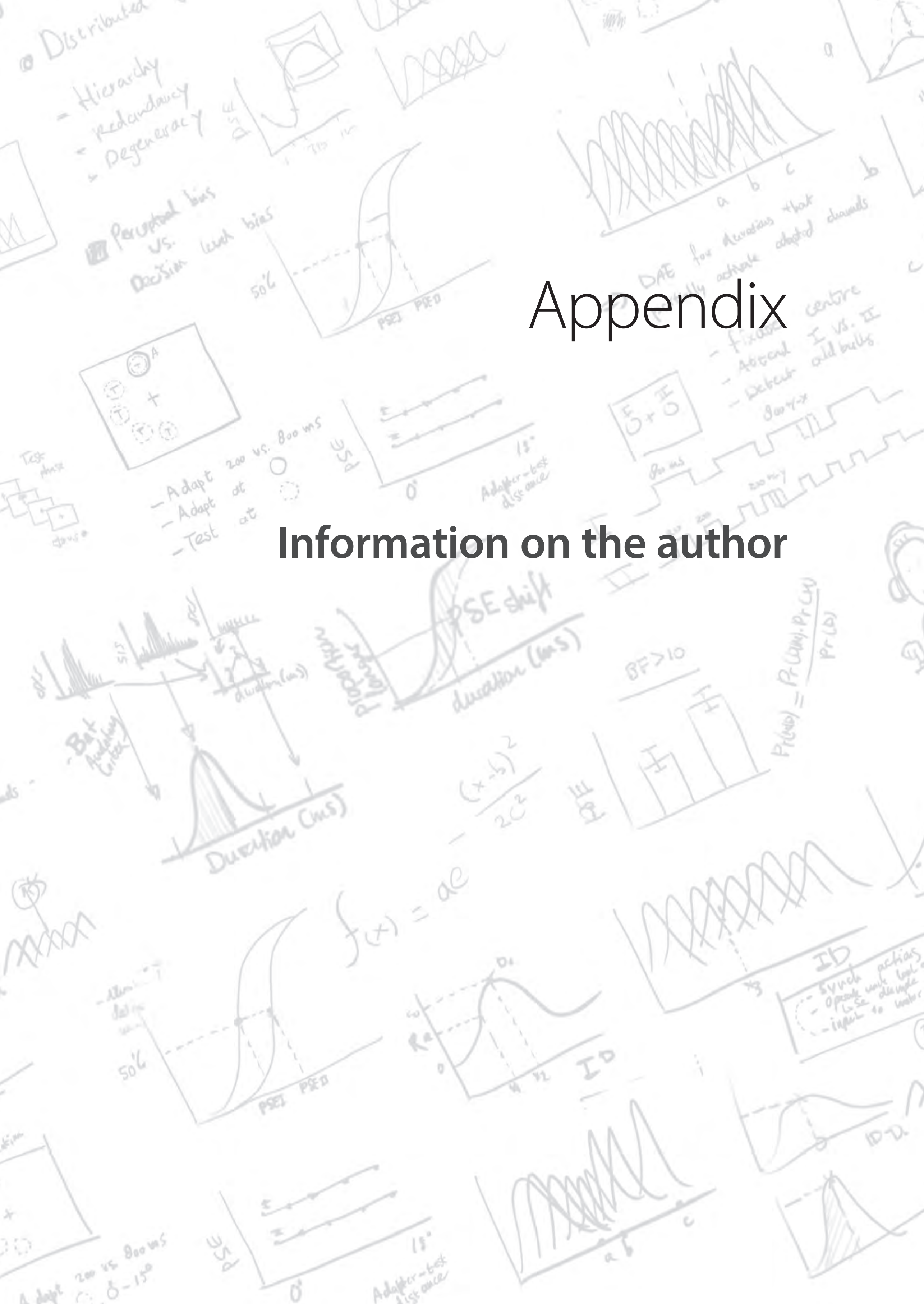
Sine, ik denk niet dat je echt geholpen hebt met het tot stand komen van deze dissertatie, maar je hebt wel van mij een beter en gelukkiger mens gemaakt. Ik verheug me op jouw reis door het leven en ik hoop dat ik daar nog heel lang onderdeel van uit mag maken.

“... A few turnings later and I was thoroughly lost. There is a school of thought which says that you should consult a map on these occasions, but to such people I merely say, ‘Ha! What if you have no map to consult? What if you have a map but it’s of the Dordogne?’ My own strategy is to find a car, or the nearest equivalent, which looks as if it knows where it is going and follow it. I rarely end up where I was intending to go, but often I end up somewhere that I needed to be.”

Douglas Adams, The Long Dark Tea-Time of the Soul



Appendix

Information on the author

Curriculum Vitae

Jim Maarseveen was born on the 20th of July 1988 in Brielle, The Netherlands. After graduating from secondary school in 2007 at the Maerlant college, he decided to study Psychology at the Erasmus University Rotterdam. Here he attained both a Bachelor (2010) and Master's (2012, graduated cum laude) degree in Biological & Cognitive Psychology. During this time, he also completed the Erasmus University Honours programme (2008-2009) and worked as a research assistant at the Embodied Cognition Lab with prof dr. Rolf Zwaan. After attaining his Master's degree he started working as a PhD student at the department of Experimental Psychology at Utrecht University under the supervision of Frans Verstraten, Chris Paffen and Hinze Hogendoorn. His work as a PhD eventually culminated in the present PhD thesis. Since 2018, Jim works as the coordinator of the labs and research support desk of the Faculty of Social and Behavioural Sciences at Utrecht University.

List of published works

Peer reviewed publications

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.

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Maarseveen, J., Hogendoorn, H., Verstraten, F., & Paffen, C. (2017). Attention mediates the encoding of duration. *Journal of Vision*, *17*(10), 189-189.

Maarseveen, J., Hogendoorn, H., Verstraten, F., & Paffen, C. (2016). Duration adaptation is position invariant. *Journal of Vision*, *16*(12), 1129-1129.

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Distributed processing
- Hierarchy
- Redundancy
- Degeneracy
$P_r(M|D) = \frac{P_r(D|M)\,P_r(M)}{P_r(D)}$
$f(x) = \frac{L}{1+e^{-k(x-x_0)}}$
IT'S ABOUT TIME...
no shift
shift
no shift
Adaptation phase
PSE shift
duration (ms)
Proportion longer
Duration (ms)
DAE for durations that partially activate adapted channels
ID
a
b
c