Human Duration Perception Mechanisms in the Subsecond Range: Psychophysics and Electroencephalography Investigations

Thesis by

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In Partial Fulfillment of the Requirements for
the degree of
Ph.D. in Computation and Neural Systems

CALIFORNIA INSTITUTE OF TECHNOLOGY
Pasadena, California

2018
(Defended November 6, 2017)

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ACKNOWLEDGEMENTS

I am deeply grateful that my advisor and mentor, Prof. Shinsuke Shimojo gave me plenty of freedom to explore different research directions until I began to embrace and grasp the study of time perception that was entirely out of my comfort zone. Needless to say, the research was a bumpy ride and it took me long enough to reach this far. I still remember that one day when I finally had a small breakthrough, my advisor just told me that “I will guide you until you can fly on your own.” This enlightenment and encouragement have accompanied me through countless obstacles since then.

I also feel lucky to receive warm and positive social support from family and many friends. My parents Santus and Amy always wish the best of me. My brother Willy constantly share with me the outlook of a career path that I may never have a chance to experience. I have enjoyed the good times with many good friends since my beginning at Caltech, including Thanh Phong Nguyen and Thuy Duong Nguyen, Prof. Aron Kamajaya and Monica Kamajaya, Dr. Raymond Liu and Dr. Nadia Herrera, and Feng Chen, as well as fun memories with my classmates Dr. Bo Chen, Dr. Daniel McNamee, Dr. Soyoung Park, Dr. Nicolette Sullivan, and Dr. Shuo Wang. The stimulating conversations with Dr. Bo Chen and the cycling adventures with Dr. Daniel McNamee were especially great times. The insights and wisdoms from Prof. Bor-Shiuan Cheng, Prof. Chou-Yu Tsai, Richard Chang, and Zoe Hsu all helped me stay on track and see my path clearer. Motivating conversations with my athletic friend William Liang always boosts my morale.

To be able to execute the research, I am indebted to several lab members and collaborators. Dr. Daw-An Wu inspired me a lot with his ingenuity in story-telling and technical skills. Along this journey, Dr. Elisa Carrus, Ondřej Zíka, Sepideh Farmani, and William Liang helped me carry out tons of cool experiments. Before the final defense, Dr. Christopher Berger and Dr. Mohammad Shehata also provided valuable inputs for my presentation.

At different stages, my exam committee members, Prof. Markus Meister, Prof. John P. O'Doherty, and Dr. Kyongsik Yun, gave me many constructive and valuable comments. I want to express my gratitude to them for their advice that broadened my horizon and pushed me forward.

As half of the discovery in science is probably completed in the process of intensive reading, writing, and thinking, up to the present I still feel thankful for the terrific English writing lessons from Prof. Arthur Woodward and Justin Xie that changed how I communicate.

Last but not the least, I appreciate the funding support from Ministry of Education, Taiwan and the National Science Foundation for making this journey possible.

ABSTRACT

In a world full of fleeting events, how do humans perceive time intervals as short as half a second? Unlike primary senses, there are no time receptors. Is subsecond time perception reconstructed from memory traces in the primary senses, or based on the output of a modality-independent internal clock? In analogy to bugs in computer programs or mutations in genetics studies, I studied two types of subjective time warp illusions in order to understand how time perception normally works. One illusion that I examined is called oddball chronostasis, which is a duration distortion effect that happens to an unusual item. The other illusion is called debut chronostasis, which is a time warp effect that occurs to the first item among other identical ones.

Regarding oddball chronostasis, we solved a theoretical dispute over its underlying mechanisms and dissociated three causes. The necessary component is top-down attention to the target item. The other two components are contingent factors. This suggests that a pure sensory modality-dependent view of time perception mechanisms is less likely.

Regarding debut chronostasis, we discovered auditory debut chronostasis and found that its illusion strength is about the same as the visual case. At first glance, this seems to suggest that time perception is independent of the primary sensory modalities. However, when visual and auditory events were compared against each other (inter-modal comparison), debut chronostasis disappeared. Therefore, modality-dependent mechanisms of time perception do exist. Further, we found a special factor that could counteract debut chronostasis and thus re-interpreted the main cause of debut chronostasis as internal duration template uncertainty. By examining both intra- and inter-modal comparisons, this uncertainty effect turned out to be a modality-independent effect. Therefore, modality-independent mechanisms of time perception also exist.

In conclusion, this dissertation work contributed to novel theoretical understanding of two types of time perception illusions. Unlike many simplified theories in the literature either holding a modality-dependent or independent view, our findings altogether indicate that

time perception involves both intra- and supra-modal stages. Future experimental work could thus target on separating intra- and supra-modal time perception mechanisms.

PUBLISHED CONTENT AND CONTRIBUTIONS

Chapter II of this thesis has been published as:

Lin, Y.-J., Shimojo, S. (2017). Triple dissociation of duration perception regulating mechanisms: Top-down attention is inherent. PLoS ONE 12(8): e0182639. doi: 10.1371/journal.pone.0182639

Y. J. L. proposed the project, co-formulated the hypotheses, designed the experiment, gathered the data, analyzed the results, prepared the initial manuscript, and participated in discussions and revisions until publication.

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NOMENCLATURE

Anti-chronostasis. The illusion of subjective time contraction (under-estimation).

Chronostasis. The illusion of subjective time expansion (over-estimation).

Chronostasis magnitude (CM). Amount of chronostasis effect. The positive direction indicates chronostasis. The negative direction indicates anti-chronostasis.

Debut chronostasis. Subjective time expansion illusion that occurs to the first item in a train of identical items.

Electroencephalography (EEG). The methodological practice to measure neural activity from electrical potentials on the scalp.

Inter-Modal. Used inter-exchangeably with cross-modal. Between two modalities.

Intra-Modal. Used inter-exchangeably with within-modal. Of the same modality.

Modality. Or sensory modality. A particular aspect for the brain to receive external input.

Oddball chronostasis. Subjective time expansion illusion of a rare or novel item lasting longer in duration than other repeated/frequent items.

Physical time. From a third-person perspective, the objective time that is measurable with cyclic physical references such as clocks.

Point of objective equality (PSE). The physical quantity of the reference item in a discrimination task.

Point of subjective equality (PSE). In a psychometric function, the physical quantity that the 50% response point maps onto.

Psychological time. From a first-person perspective, the subjective time that is measurable with subjective report or responses.

Psychometric function. A sigmoidal function that describes how the probability of a human observer’s response varies with a specific physical quantity.

Supra-Modal. Used inter-exchangeably with meta-modal. Beyond sensory modalities. In the cortical sense, this may refer to association cortex mechanisms.

Time-frequency representation (TFR). Windowed Fourier transform results of time series data.

Chapter 1

INTRODUCTION

1.1 The Time Sense

How humans could perceive time in the first place is an intriguing question in neuroscience. Unlike the five primary senses—sight, hearing, taste, smell, and touch—where each of them has receptors receiving external stimulation in the form of either matter or energy, there is simply no clearly defined "time receptor." This is mainly because from the perspective of physics, time and space are where matter and energy exist and interact. Time is simply more fundamental in its ontological status.

Yet humans perceive time without obvious difficulties. One intuitive explanation is that time perception is based on measures built inside the body such as proprioception. In other words, perceived time could be a measure of internal change in disguise. On the other hand, there are a handful of subjective duration distortion phenomena, which some would dub as subjective time warp by analogy to physics, suggesting that subjective duration is not only influenced by internal cognitive state but also by external event context. Therefore, examining both endogenous and exogenous factors is vital to the understanding of how time perception works.

1.2 Ranges of Time Sense

Not all timing behavior and time perception are associated with the same set of biological clocks. Humans can process temporal information spanning over at least 12 orders of magnitude (Mauk & Buonomano, 2004). Across species, including mammals, ring doves, and fruit flies, about three major groups of mechanisms exhibit their own characteristic variability in timing behavior (Buhusi & Meck, 2005, but see Lewis & Miall, 2009). These three groups of mechanisms are circadian timing (about 24 hours), interval timing (spanning across half a second and a day), and millisecond timing (ranging from tens of milliseconds to about one second). Circadian timing has the lowest overall ratio of estimation error (about 1~10%); the estimation error ratio of millisecond timing (about 3~40%) and interval timing are higher (about 1~30%). Gibbon, Malapani, Dale, and Gallistel (1997) further suggested that the supra- and subsecond intervals could involve different mechanisms based on distinct coefficients of variation in these two time ranges. To corroborate the idea, Lewis and Miall (2003) carried out an fMRI study with duration discrimination as the main task and visual discrimination as the control task, using 0.6 and 3 seconds to represent sub- and supra-second intervals. Their data showed that sub- and supra-second time measurements have shared neural substrates, but each range has its own additional components. Based on that, they suggest subsecond interval discrimination recruit more automatic systems while supra-second interval discrimination involve other systems that require higher cognitive control.

While the biological basis of circadian rhythm is relatively well understood, the neural mechanisms of interval timing and millisecond timing are much less clear. Circadian rhythm is rooted in a genetic transcription-translation negative auto-feedback loop utilized by the suprachiasmatic nucleus in the brain (for reviews, see King & Takahashi, 2000; Saper, 2013). On the other hand, interval timing involves distributed cortical and subcortical mechanisms (Wiener, Turkeltaub, & Coslett, 2010). How the neural activities relate to subjective interval duration and what role each neural area plays are still active issues being investigated and discussed. The distributed nature of interval perception mechanisms especially poses knowledge gaps and theoretical challenges.

Therefore, to reduce the number of unknown factors, in my thesis work I focused on the subsecond time perception and provided new experimental insights. In the next few sections, I will briefly review the latest theoretical advancements, highlight ongoing disputes, and point out why duration distortion phenomena are particularly useful in tackling the theoretical problems.

1.3 Theories of Subsecond Time Perception

The dominant information processing framework of time perception theories in early days postulates an internal clock, along with subsequent information processing components such as a counter (accumulator), a memory store, and a comparator for reaching decision (Treisman, 1963). Fig 1.1 illustrates the theoretical components. Along with the discovery of constant coefficient of variation of response distributions in animal timing studies ("the scalar property," after Gibbon, 1977, which is actually a form of Weber's Law), its full mathematical properties were formulated by Gibbon, Church, and Meck (1984). Since then, this internal-clock-based scalar timing theory (or the pacemaker-accumulator model) has been widely applied to human and animal timing studies with supporting evidence from behavioral as well as pharmacological studies (for a brief review, see Buhusi & Meck, 2005).

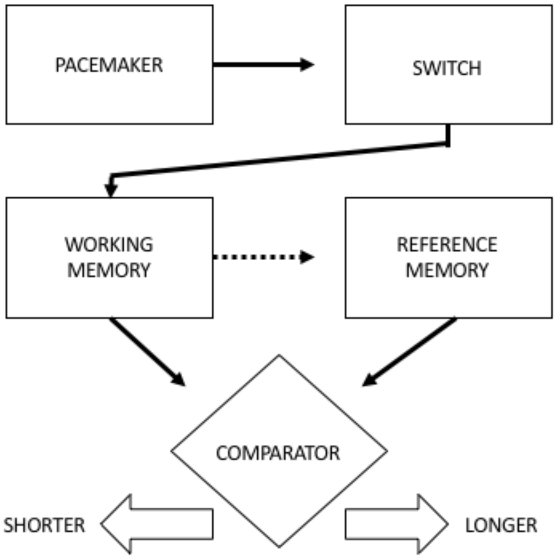

Figure 1.1 The information processing framework of the scalar timing theory (or the pacemaker-accumulator model, adapted from Treisman, 1963; Gibbon, Church, and Meck, 1984). It starts with an internal pacemaker which sends pulses, gated by the switch, to the working memory (the accumulator). Comparison of the duration memory traces between the working memory and the reference memory leads to the final judgment.

The postulates of the scalar timing theory (Gibbon et al., 1984) makes several interesting predictions. If an additive effect on the mean of response distribution is found (independent of the physical duration), it can be attributed to the advancing or delaying of the switch onset or offset when the accumulator starts and stops counting pulses from the pacemaker. If a multiplicative effect (dependent on the physical duration) is found instead, it can be attributed to the pacemaker rate change, or noises in the accumulator stage.

Despite of the quantitative explanatory power of the scalar timing theory, it does not directly lead to predictions regarding specific brain regions as the information processing nodes. Based on newly discovered evidence, subsequent neuroscientists proposed various candidates of the internal clock locus. Matell and Meck (2004) specified a striatal-beat-frequency (SBF) model which relies on medium spiny neurons located in the dorsal striatum, whose converging inputs make them ideal coincidence detectors. Walsh (2003) described the parietal cortex as a common magnitude system that deals with quantities such as space, time, and numbers. Eagleman and Pariyadath (2009) hypothesized that sensory cortical neural response amplitude directly maps onto subjective duration. Merchant, Harrington, and Meck (2013) depicted a generalized picture and interpreted the cortico-thalamic-basal ganglia circuit as the core timing system, while other neural structures serve as context-dependent areas. For example, the cerebellum, the primary visual, auditory, and somatosensory areas may be recruited in motor, visual, auditory, and tactile timing tasks, respectively. Indeed data-driven meta-analysis from PET and fMRI studies exhibited the distributive nature of brain areas involved in time perception, and it turned out that the bilateral supplementary motor area (SMA) and the right inferior frontal gyrus (rIFG) were shared among supra- and subsecond motor and perceptual timing tasks (Wiener, Turkeltaub, & Coslett, 2010). However, so far there is still no strong consensus on whether there is a unified internal clock in the brain. At least this is the beginning to bridge the gap between the scalar timing theory and the neural imaging results.

1.4 Major Debates over Subsecond Interval Perception Mechanisms

1.4.1 Are Internal Timing Mechanisms Intra- or Supra-Modal?

Since every perception and action has a temporal aspect, to what extent does time perception depend on the stimulus modalities? As reviewed earlier, subsecond interval perception is not just the manifestation of the same set of biological clocks underlying circadian rhythm. The answer to this question arguably determines the first premise of interval perception theories, and provides unique angles in interpreting neuroscientific data. Starting from this question, Ivry and Schlerf (2008) gave an especially sharp conceptual overview of different flavors of time perception models. They classified existing theories into two camps. The traditional view is that there are dedicated (supra-modal) mechanisms for time perception per se. For example, the internal clock idea along with the pacemaker-accumulator model (Treisman, 1963; Gibbon et al., 1984) and the SBF (striatal-beat-frequency) model (Matell & Meck, 2004) belong to this category. By contrast, the modern viewpoint is that time perception could be intrinsic in modality-specific information processing so that no dedicated mechanism for time perception is required. For example, Buonomano (2000) presented a model that temporal information can be extracted from synaptic weights. The sensory neural response magnitude hypothesis by Eagleman and Pariyadath (2009) also falls into this category.

Given that these two perspectives are not mutually exclusive and the fact that time perception related neural mechanisms are distributed, it is also reasonable that a complete picture of time perception may as well be a synthesis of both the dedicated (supra-modal) and intrinsic (intra-modal) viewpoints. Whichever is true, Ivry and Schlerf (2008) pointed out that examining cross-modal training transfer could be a starting point. For example, cross-modal transfer may depend on the activity of association cortices (supra-modal view) or connectivity between primary sensory areas (intra-modal view).

In our view, a highly interesting hint comes from direct comparisons between visual and auditory event durations. Multiple studies have reported a peculiar phenomenon that the duration of auditory events appears to be subjectively longer than those of visual events even when saliency across these two modalities is matched (Behar & Bevan, 1961; Goldstone & Goldfarb, 1964; Goldstone & Lhamon, 1974; Goldstone, Lhamon, & Sechzer, 1978; Loeb, Behar, & Warm, 1966; Penney, Gibbon, & Meck, 2000; Rammsayer, Borter, & Troche, 2015; Sebel, & Wilsoncroft, 1983; Wearden, Edwards, Fakhri, & Percival, 1998; Zélanti & Droit-Volet, 2012). Human observers often reported that intra-modal interval comparisons were easy (within the auditory modality the easiest) while inter-modal comparisons were hard. These participants' feedback was indeed backed by the measured discrimination sensitivity (e.g. Ulrich, Nitschke, & Rammsayer, 2006).

The result that inter-modal duration comparisons are harder almost already implies that there exist within-modal mechanisms. Two studies applied the scalar timing model and concluded that this phenomenon can be attributed to differences in pacemaker speed (Ulrich et al., 2006; Wearden et al., 1998). However, if the visual and auditory cortices do drive the internal pacemaker at different rates, then the full picture must incorporate modality-specific stages. Alternatively, if interval perception is purely modality-specific, inter-modal duration comparisons can be realized at association cortices or communications between sensory cortices.

1.4.2 Does Subsecond Duration Perception Depend More on Perceptual or Cognitive Factors?

Although Lewis and Miall (2003) suggested that subsecond duration perception involve more automatic than cognitively controlled factors, theories behind some interesting subjective duration distortion phenomena, as will be introduced in section 1.5, suggest that many cognitive factors may be at play even in the subsecond range.

1.5 Subjective Duration Distortion (SDD) Phenomena

Just as bugs in computer programs, or mutations in genetics studies, time illusions are valuable for peeking into the underlying rules or mechanisms of time perception. Time illusions are often dubbed as subjective time warp or subjective duration distortion. In the subsecond range, perceived time is surprisingly prone to distortion due to multiple external and internal factors. The amount of subjective duration distortion at the hundreds of milliseconds range is mostly around 10-15%. From then on, we will use the term *chronostasis* to refer to the general subjective time expansion (over-estimation) phenomenon in the remainder of this thesis. The term chronostasis was first introduced by Yarrow and colleagues (Yarrow et al., 2001). To refer to the opposite case, we will term subjective time contraction (under-estimation) phenomenon as anti-chronostasis.

Some well-known external factors include 1) non-temporal stimulus properties, such as luminance (Goldstone, Lhamon, & Sechzer, 1978; Brigner, 1986), size (Xuan, Zhang, He, & Chen, 2007), visual flicker (Herbst, Javadi, van der Meer, & Busch, 2013), auditory flutter (Yuasa & Yotsumoto, 2015), accompanying auditory click train (Penton-Voak, Edwards, Percival, & Wearden, 1996), motion onset (Kanai & Watanabe, 2006), and the apparently longer duration of auditory than visual stimuli under the same physical duration (e.g. Goldstone & Lhamon, 1974), and 2) stimulus temporal context such as being the first, the last item (e.g., Rose & Summers, 1995), an odd one (e.g., Tse, Intriligator, Rivest, & Cavanagh, 2004), a repeated one (e.g., Pariyadath & Eagleman, 2008), or a later one (Kim & McAuley, 2013) in a multiple item sequence.

On the other hand, internal factors include 1) location-specific adaptation (Johnston, Arnold, & Nishida, 2006), 2) concurrent task interference (Brown, 1997), 3) attention orienting (e.g., Coull, Frith, Büchel, & Nobre, 2000; Lin & Shimojo, 2017; Mattes & Ulrich, 1998; Rohenkohl, Coull, & Nobre, 2011; Tse et al., 2004), 4) working memory (Pan & Luo, 2012), 5) emotion (e.g., Stetson, Fiesta, & Eagleman, 2007), and 6) relative timing between voluntary actions and temporal perception (e.g., Hagura, Kanai, Orgs, & Haggard, 2012; Park, Schlag-Rey, & Schlag, 2003; Yarrow, Haggard, Heal, Brown, & Rothwell, 2001).

Among all the phenomena listed above, I focused on two specific phenomena because they shared similar theoretical disputes (details in the next section) and related directly to the two major theoretical disputes reviewer earlier. The first phenomenon is that the first item in a multiple item visual sequence appears to last longer (e.g., Rose & Summers, 1995) (from then on, I will term this debut chronostasis, after the term chronostasis coined by Yarrow et al., 2001). The second phenomenon is that the odd item that stands out from other repeated items in a sequence appears to last longer (e.g., Tse et al., 2004) (which I will refer to as oddball chronostasis in the remainder of the thesis).

1.6 Dissertation Overview

Followed by the background information in Chapter I, Chapter II will be about oddball chronostasis psychophysics; Chapter III and IV will be about debut chronostasis psychophysics. Chapter V will be about oddball chronostasis electroencephalography (EEG). Since the initial discovery of debut chronostasis (Tse et al., 2004), Chapter II presents critical psychophysical experiments as a solution to the dispute among three theories; Chapter III establishes a novel hypothesis of the debut chronostasis mechanisms. Chapter IV extends the original visual debut chronostasis phenomenon (Rose & Summers, 1995) to untested auditory as well as cross-modal domains, and reveals intra- and supra-modal stages of interval perception. Chapter V presents a novel method in interval perception with EEG to further support the conclusions in Chapter II. The contributions, limitations, and future directions are discussed in Chapter VI.

Chapter II

TRIPLE DISSOCIATION OF DURATION PERCEPTION REGULATING MECHANISMS: TOP-DOWN ATTENTION IS INHERENT

2.1 Abstract

The brain constantly adjusts perceived duration based on the recent event history. One such lab phenomenon is subjective time expansion induced in an oddball paradigm (“oddball chronostasis”), where the duration of a distinct item (oddball) appears subjectively longer when embedded in a series of other repeated items (standards). Three hypotheses have been separately proposed but it remains unresolved which or all of them are true: 1) attention prolongs oddball duration, 2) repetition suppression reduces standards duration, and 3) accumulative temporal preparation (anticipation) expedites the perceived item onset so as to lengthen its duration. We thus conducted critical systematic experiments to dissociate the relative contribution of all hypotheses, by orthogonally manipulating sequences types (repeated, ordered, or random) and target serial positions. The participants’ task was to judge whether a target lasts shorter or longer than its reference. The main finding was that a random item sequence still elicited significant chronostasis even though each item was odd. That is, simply being a target draws top-down attention and induces chronostasis. In Experiments 1 (digits) and 2 (orientations), top-down attention explained about half of the main effect while saliency/adaptation explained the other half. Additionally, for non-repeated (ordered and random) sequence types, a target with later serial position still elicited stronger chronostasis, favoring a temporal preparation over a repetition suppression account. By contrast, in Experiment 3 (colors), top-down attention was likely the sole factor. Consequently, top-down attention is necessary and sometimes sufficient to explain oddball chronostasis; saliency/adaptation and temporal preparation are contingent factors. These critical boundary conditions revealed in our study serve as quantitative constraints for neural models of duration perception.

2.2 Introduction

Perceiving time is special to humans because time itself is not a physical entity commensurate with matter and energy. Accordingly, the subjective sense of time may rely upon inferences from primary senses as well as a person's cognitive state. In the subsecond range of time perception, a growing body of research has shown that the perceived duration of an event not only depends on its temporal context but also on the observer's psychological activities. For example, in a string of events, humans tend to observe particular events as lasting longer, such as the first or the last in the sequence (Rose & Summers, 1995), or when there is an odd event in the context (Tse, Intriligator, Rivest, & Cavanagh, 2004). The subjective expansion of time is also experienced when we switch hearing from one ear to the other (Hodinott-Hill, Thilo, Cowey, & Walsh, 2002), during the first moment after we shift our gaze to read a clock (e.g., Yarrow, Haggard, Heal, Brown, & Rothwell, 2001), and during the moment right before baseball or tennis players strike the ball (Hagura, Kanai, Orgs, & Haggard, 2012). These reported subtypes of subjective time expansion effects may share related neural underpinnings, reflecting how the brain constructs and regulates perceived time.

Prior research has revealed that time perception involves multiple cortical and subcortical brain areas (e.g., Buhusi & Meck, 2005; Grondin, 2010; Wiener, Turkeltaub, & Coslett, 2010). A clear picture of how these areas interact is still lacking. The aforementioned phenomena thus provide a window into how the brain takes bottom-up, stimulus-driven and top-down, goal-driven factors both into account. In this study, we focus on the mechanisms of subjective time expansion with an oddball paradigm. It is a perceptual case that does not concern action-related factors, and arguably one of the most theorized and experimented case among related phenomena. In such a paradigm, the duration of a novel item (oddball) appears subjectively longer than that of other repeated items (standards) in a sequence (Tse et al., 2004). For the sake of simplicity, we will refer to this specific phenomenon as 'oddball chronostasis' in the remainder of this article, following the generic term 'chronostasis' first introduced by Yarrow et al. (2001) to describe the situation that the second hand of a clock seems to have stopped (i.e., subjective time expansion).

In the literature, two major theories were proposed to explain oddball chronostasis that resonates with this top-down and bottom-up distinction. One is the attention theory, which states that attention increases the subjective duration of the oddball (New & Scholl, 2009; Tse et al., 2004). The other is the repetition suppression theory, which instead states that through adaptation or predictability, the subjective duration of the standards reduces (Cai, Eagleman, & Ma, 2015; Pariyadath & Eagleman, 2007, 2012; Schindel, Rowlands, & Arnold, 2011). By contrast, the oddball stimulus appears longer because it is less susceptible to the repetition suppression.

Several previous key findings support the attention hypothesis. First, Tse et al. (2004) discovered that the amount of visual duration distortion in general rose with reference duration with an initial local peak around 225 msec followed by a dip around 375 msec until it saturated beyond 1000 msec, consistent with the signature of transient and sustained components of attention (e.g., Nakayama & Mackeben, 1989; Remington, Johnston, & Yantis, 1992). Given that attention orienting takes time, the attention hypothesis could also explain why anti-chronostasis (subjective time compression) occurred when the reference duration was less than about 120 ms. Second, Tse and colleagues (2004) found that oddball chronostasis in visual and auditory cases shares similar patterns, which is consistent with a central mechanism account such as attention. Third, New and Scholl (2009) found that the occurrence of an oddball dilated the perceived duration of another item simultaneously presented at a different location and the effect was unaffected by target-oddball spatial distance or whether the oddball and the target item belong to the same object. They thus concluded that this global time expansion effect might reflect increased arousal driven by attention.

On the other hand, other existing evidences support the repetition suppression hypothesis more. First, oddball chronostasis scales with oddball's serial position (Kim & McAuley, 2013; Pariyadath & Eagleman, 2012; Sadegh, Pariyadath, Apte, Eagleman, & Cook, 2011).

Second, oddball chronostasis scales with feature discrepancy between the oddball and the standards (Kim & McAuley, 2013; Pariyadath & Eagleman, 2012; Schindel et al., 2011). Third, oddball chronostasis can be elicited by brightness oddballs dimmer than the standards (Schindel et al., 2011). Therefore, the underlying mechanisms of repetition suppression may involve low-level adaptation as well as high-level prediction error of stimulus content or position.

Interestingly, the attention and the repetition suppression hypotheses are in fact logically compatible. The former predicts the subjective expansion of the oddball duration while the latter subjective compression of the standard duration. It means that these two hypotheses can both possibly contribute to the oddball chronostasis, and that they can be directly compared in a single experiment. First, the attention effect can be broken down into bottom-up saliency and top-down attention (c.f. Tse et al., 2004). Second, the repetition suppression effect can be divided into adaptation as well as prediction error (Schindel et al., 2011). Therefore, the four new hypotheses in question become top-down attention, bottom-up saliency, adaptation, and prediction error. Theoretically saliency and adaptation are different, but indistinguishable empirically in the operational definition of the following experiments. Accordingly, we regroup the hypotheses above into three instead (top-down attention, saliency/adaptation, and prediction error) and aim to identify their relative contributions across experimental conditions.

To dissociate these refined hypotheses, we measured participants' chronostasis magnitude (CM, which quantifies how large the subjective time expansion of a target is when compared with a reference, see *Materials and Methods* for details) with three types of item sequences: repeated, ordered, and random (Fig 2.1A). The repeated condition was the classic oddball paradigm. The standards were repeated and the oddball was distinct from the standards. As Fig 2.2A illustrates, in the most comprehensive scenario, top-down attention, saliency/adaptation, and prediction error could all be underlying factors. In the ordered condition, items never repeated; thus, this condition excluded adaptation/saliency as an explanation. The target was the item that did not follow the regularity. In the random condition, the observers were pre-instructed which item would be the target while the other items were random and carried no information about what the target would be. Compared with an ordered sequence, a random sequence further excluded prediction error and thus singled top-down attention out as an underlying cause. Therefore, contrasting CM across sequence types could unravel which factors are critical. Fig 2.2A-D depict several possible scenarios of the sequence type effect.

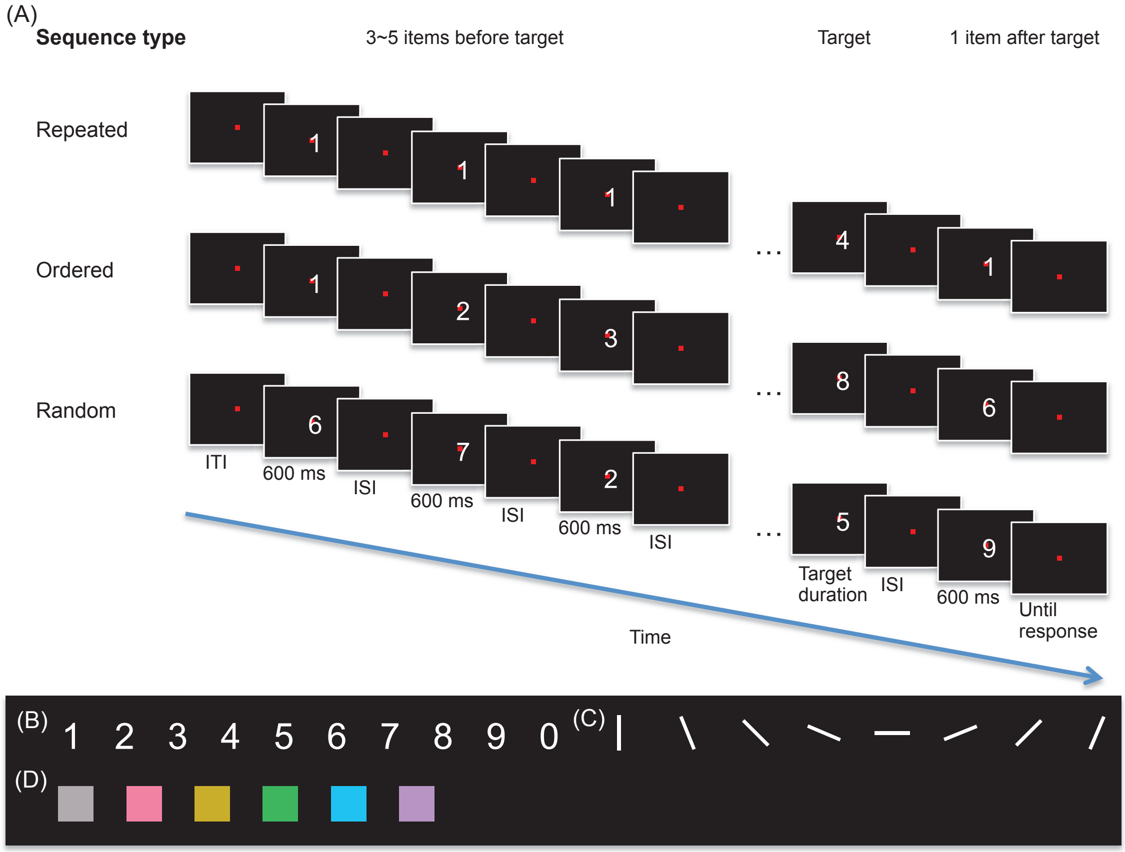

Fig 2.1. Paradigm and stimuli.

(A) In each type of item sequences, the observers performed a duration discrimination task between the target and its reference to estimate the amount of duration distortion (see Methods for details). (B-D) Stimulus sets in Experiments 1, 2, and 3, respectively.

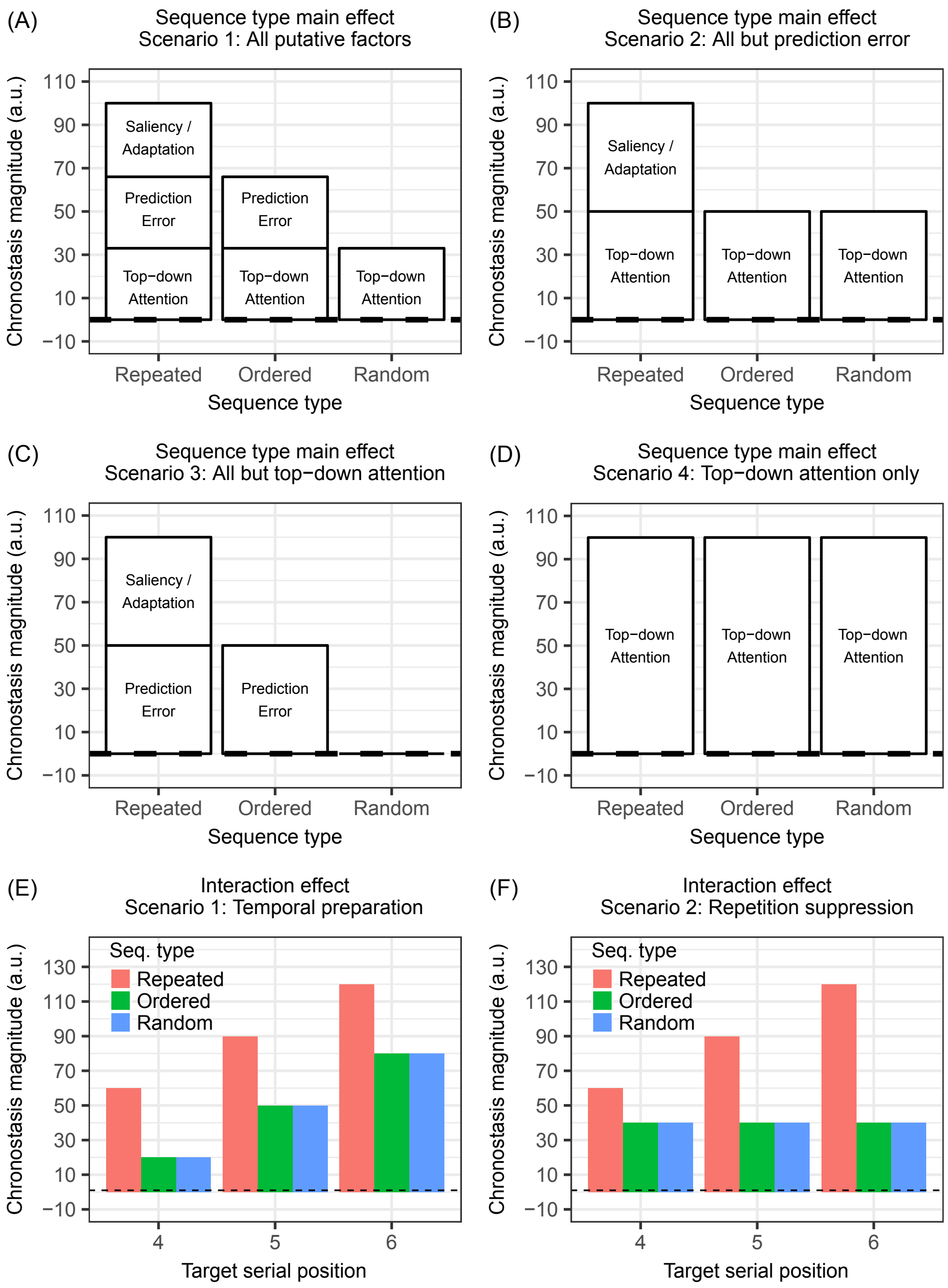

Fig 2.2. Theoretical predictions of results.

Vertical axis is chronostasis magnitude (the amount of subjective time expansion, see methods and supplementary methods for details). (A-D) Four likely scenarios of the sequence type main effect, given the controversy between the attention and the repetition suppression theories. (E-F) Two likely scenarios of the interaction effect between sequence types and target serial positions, given the controversy between temporal preparation and repetition suppression theories. See introduction for details of the rationale and the experimental design. The predictions here assume additive and independent components.

Apart from the main issue regarding the origin of oddball chronostasis, there is also a side issue about what mechanism modulates it. Several previous studies (Kim & McAuley, 2013; Pariyadath & Eagleman, 2012; Sadeghi et al., 2011) have reported that the larger the serial position of the oddball is inside a sequence, the greater the CM, and the effect could eventually saturate. Two explanations have been proposed. One is the temporal preparation account by Kim and McAuley (2013) which states that oddball chronostasis at least partly originates from how early one could detect the onset of the target item. Assuming that the offset is unaffected, an apparently earlier onset is tantamount to longer perceived duration. Using an oddball detection task, their data did reveal such a negative correlation between response time and CM. The other is the repetition suppression account (Cai, Eagleman, & Ma, 2015; Pariyadath & Eagleman, 2007, 2012; Schindel, Rowlands, & Arnold, 2011) as described earlier, which states that the more the repetition, the greater the CM. However, in previous experiments (Kim & McAuley, 2013; Pariyadath & Eagleman, 2012; Sadeghi et al., 2011) reporting this target serial position effect, standards were always repeated. Thus, a critical test between these two hypotheses was missing. By contrast, in our design, the sequence type and the target serial position were orthogonally manipulated. If the temporal preparation hypothesis were true, CM would grow with target serial position regardless of sequence type (Fig 2.2E), resulting to no interaction effect. Conversely, if the repetition suppression hypothesis were true, CM would grow with target serial position in the repeated but not in the ordered and the random sequence condition, leading to significant interaction effect (Fig 2.2F).

In Experiment 1, we started from digits as stimuli (Fig 2.1B), as these distinct sequence types can be intuitively constructed (Fig 2.1A). The results demonstrated that half of the oddball chronostasis could be explained by top-down attention, while the other half by bottom-up saliency or adaptation, but not prediction error. To determine whether the findings can be generalized to lower level visual attributes, Experiment 2 tested orientations as stimuli, which were also adopted in several previous studies (Cai, Eagleman, & Ma, 2015; Pariyadath & Eagleman, 2012; Schindel, Rowlands, & Arnold, 2011). To further disentangle adaptation from saliency, Experiment 3 examined colors because they are highly salient and draw stimulus-driven attention rather automatically. The results revealed that top-down attention is sufficient as an explanation for oddball chronostasis among colors. The overall implications for top-down and bottom-up mechanisms underlying chronostasis are discussed.

2.3 Materials and Methods

2.3.1 Participants

All experiment protocols were approved by the institutional review board of California Institute of Technology (Caltech). The observers were drawn from the Caltech brain science subject pool, which mainly consisted of Caltech and Pasadena City of College students. In Experiment 1, there were 16 observers (8 female; 14 naïve; 20-54 years; M = 29.8; SD = 8.1). In Experiment 2, there were 19 participants (9 female; 18 naïve; 18-59 years; M = 27.5; SD = 10.5). In Experiment 3, there were 14 participants (6 female; 14 naïve; 18-41 years; M = 25.4; SD = 7.6). All participants provided written informed consent before the experiments. The naïve participants were paid for their cooperation. Participants of Experiment 3 all passed an Ishihara color blindness test.

2.3.2 Apparatus

The stimuli were presented using a Philips Brilliance 202P7 monitor in Experiments 1 and 3, and a Lacie Electron 22 Blue IV monitor in Experiment 2. The screen resolution was set at 800 (H) x 600 (V) with frame rate 120Hz. The viewing distance was 70cm. The stimuli presentation code was written in Python with PsychoPy toolbox (Peirce, 2007) under Mac OS X. To ensure that the timing was precise, a preemptive setting was adopted to override other background processes. All Commission Internationale d'Éclairage (CIE) 1931 chromaticity (x, y) and luminance (Y) values were measured by a Konica Minolta CS-100A colorimeter.

2.3.3 Design

The two independent variables sequence type and target serial position were factorially crossed within subjects. There were 3 levels of sequence types (repeated, ordered, random) in Experiments 1 and 2, and 2 levels (repeated, random) in Experiment 3. There were 3 levels of target positions (4th, 5th, 6th) in all experiments. The dependent variable was chronostasis magnitude (CM), whose measurement is described in the later subsections. Therefore, CM was analyzed with a two-way analysis of variance (ANOVA) in each experiment.

2.3.4 Stimuli

All stimuli were presented at the center of the screen where there was a constant red (CIE x = 0.614, y = 0.342, Y = 26.1) fixation point spanning 0.1° (H) x 0.1° (V) visual angle at the center of the screen. The background was black. In Experiment 1, the stimuli set comprised white digits 0 to 9 each spanning 1.0° (H) x 1.5° (V) visual angle (Fig 2.1B). In Experiment 2, the stimuli set comprised bars spanning 5° (H) x 1° (V) visual angle with one of the 8 orientations: 0°, 22.5°, 45°, 67.5°, 90°, 112.5°, 135°, and 157.5° (Fig 2.1C). In the ordered condition, the orientation sequence followed either a clockwise or a counter-clockwise order, where the step between stimuli was either -22.5° or 22.5°. The target was the item that deviated from the expected regularity by skipping ahead or going backwards. To remain perceptual consistency, the last item resumed the regularity from the target rather than the items preceding the target. In Experiment 3, the stimuli set comprised squares spanning 4° (H) x 4° (V) visual angle with one of the 6 nominally isoluminant colors: red (x =0.39, y = 0.31, Y = 61.7), yellow (x =0.43, y = 0.47, Y = 61.7), green (x =0.26, y = 0.47, Y = 61.7), blue (x =0.20, y = 0.28, Y = 61.7), purple (x =0.29, y = 0.24, Y = 61.7), and gray (x =0.31, y = 0.33, Y = 61.7) (Fig 2.1D). Unlike Experiments 1 and 2, Experiment 3 did not include an ordered condition since there was not a clear way to order the colors. The item colors were specifically chosen to be isoluminant because it was known that stimulus luminance could affect its perceived duration (e.g., Goldstone, Lhamon, & Sechzer, 1978).

2.3.5 Procedure

The dependent variable CM was derived from the psychometric function estimated by the method of constant stimuli (see the subsection below for details). Thus, the participants' task was to discriminate the duration between the target item and its reference, which was the item just before it (Fig 2.1A). They were forced to make their best guess and to choose either target perceived "longer" or "shorter" using one of two keys on the computer keyboard.

In each trial, 5 to 7 items were presented one at a time, as the target serial position was between the 4th and the 6th, and an additional item was presented after the target (Fig 2.1A). We specifically avoided using the first or the last item as the target or the reference to avoid the potential confounding chronostasis effects elicited by the first and the last stimulus (e.g., Rose & Summers, 1995), as in van Wassenhove and colleagues' oddball chronostasis study (van Wassenhove, Buonomano, Shimojo, & Shams, 2008). The participants were also instructed to respond only after all items had been presented. This long gap between the target item presentation and the response helped avoid chronostasis induced by action preparation (e.g., Hagura et al., 2012). Duration of all items except the target was fixed at 600 ms. Centered around that standard duration, the target duration varied in 8 levels from 250 to 950 ms in 100 ms steps to avoid inflation of CM caused by asymmetric distribution (Seifried & Ulrich, 2010). Each inter-stimulus interval (ISI) was random, chosen from a uniform distribution between 250 and 500 ms. Each inter-trial interval (ITI) was random, chosen from a uniform distribution between 700 and 1100 ms.

Every participant was tested in 3 sessions, where each session comprised a practice block and 10 blocks of trials of a given sequence type. The order of sequence types was random per participant. A session typically took about 40 minutes. The participants were always given two separate days to finish all 3 sessions. Each session had a sequence type specific experimental instruction, followed by a practice block of 6 trials, and experiment blocks (10 in Experiments 1 and 2; 9 in Experiment 3). The practice trials were from the conditions of shortest (250 ms) and longest (950 ms) target durations and were excluded from analysis. Each of the experiment blocks contained one repeat of all 24 combinations of 3 target serial position and 8 target durations, whose order was randomly shuffled. Before each block, an instruction screen indicated the chance to take a short break.

The actual items per trial depended on the sequence type (Fig 2.1A). The repeated condition was the classical oddball paradigm, where all items except the target were the same. Thus, the oddball was the target. All items were randomly redrawn from the stimulus set per trial. In the ordered condition, the sequence always was ascending and started from 1. The target was the item that deviated from the expected regularity. In the random condition, the target item was randomly chosen from the stimulus set per block and prompted in the block instruction. Each of the standard items was sampled with replacement from the stimulus set excluding the target stimulus.

2.3.6 Psychometric Function and Chronostasis Magnitude

In each sequence type and target serial order combination, the probability of a participant reporting the target as subjectively longer than the reference were calculated. A cumulative Gaussian distribution was fitted to those data to estimate psychometric functions. The point of subjective equality (PSE) of each condition was the corresponding physical duration when the probability was 0.5 on the psychometric function. Chronostasis magnitude was thus defined as CM = reference duration - PSE. For example, a 500 ms target subjectively equivalent to a 600 ms reference this way indicates CM of 100 ms.

2.4 Results

2.4.1 Experiment 1: Digits

Crossing the factors sequence type and target serial position resulted in 9 conditions per participant. A two-way 3 (sequence type) x 3 (target position) repeated measures ANOVA was performed on the measured CM. Our refined hypotheses predict that the sequence type main effect on CM could fall into one of the four scenarios as in Fig 2.2A-D, resolving which of the top-down attention, saliency/adaptation, and prediction error hypotheses are true. The interaction effect between these two factors could also fall into either scenario as in Fig 2.2E-F, suggesting whether the temporal preparation or the repetition suppression hypothesis is more likely.

Fig 2.3 summarizes the results (N = 16) from Experiment 1. The main effect of sequence types was significant ($F_{2,30} = 5.42$, $P < 0.01$, $\eta_p^2 = 0.27$) (Fig 2.3A). Tukey post-hoc tests revealed that CM significantly differed between the repeated and the ordered conditions ($Z_{1,30} = 3.01$, $P < 0.01$), between the repeated and the random conditions ($Z_{1,30} = 2.78$, $P < 0.05$), but not between the ordered and the random conditions ($Z_{1,30} = -0.22$, $P = 0.97$). Since in the random sequence condition, the block-specific targets were defined at the beginning of each block, to verify that participants correctly memorized the target while performing the task, every block was broken into two halves. PSEs derived from the first and the second halves were compared with a two-tailed paired t-test. The non-significant difference ($t_{15} = 0.92$, $P = 0.37$) suggested that participants were able to perform the task with robust memory of the targets. A one-tailed paired t-test further showed that CM in the random condition significantly differed from 0 ($t_{15} = 1.76$, $P < 0.05$). The data pattern matched the prediction in Fig 2.2B. Therefore, it suggests that both top-down attention and saliency/adaptation, but not prediction error, are the necessary underlying factors of oddball chronostasis at least for digits stimuli. The exclusion of prediction error was in line with the conclusion of Cai and colleagues (2015) that high-level stimulus content prediction may not be an underlying factor. Our experimental design and data further showed that top-down attention and saliency/adaptation contributed about equally. Pearson's correlation of CM across participants between sequence types also strengthened this conclusion. The correlation was significant between the repeated and the ordered conditions ($r = 0.72$, $P < 0.01$), between the repeated and the random conditions ($r = 0.83$, $P < 10^{-4}$), and between the ordered and the random conditions (r = 0.78, $P < 0.001$) (Fig 2.3B-D). It suggests that chronostasis among those three sequence types share a common mechanism, which is likely top-down attention.

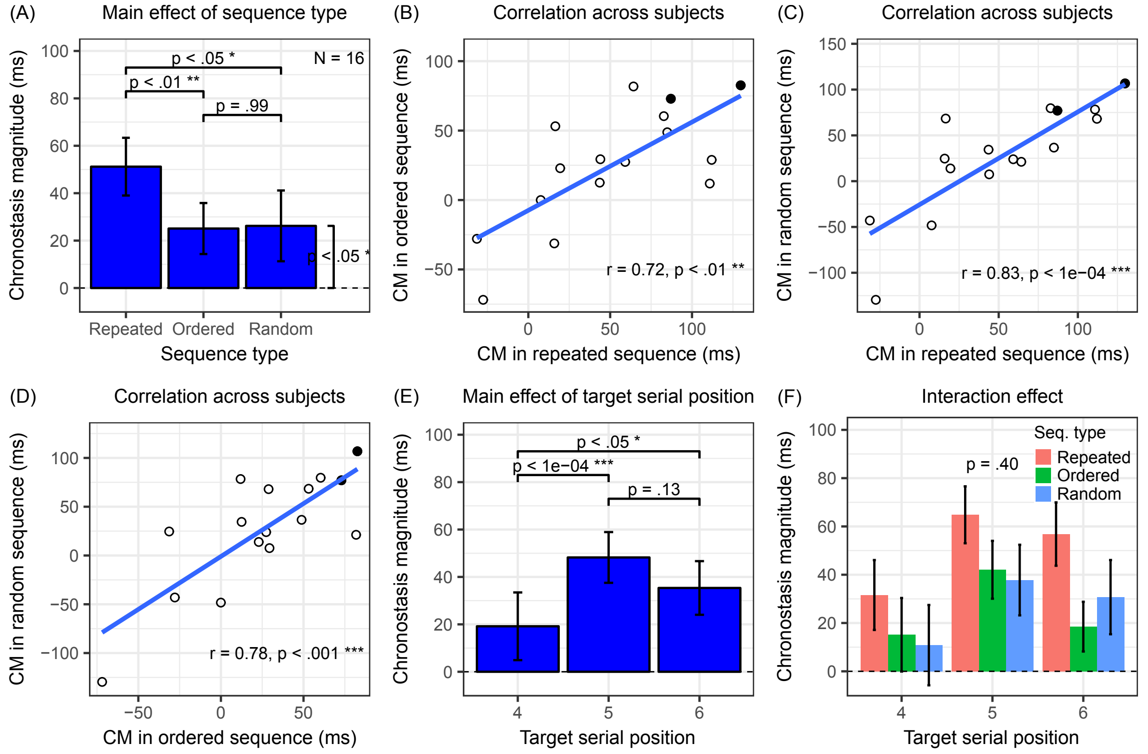

Fig 2.3. Results from Experiment 1 (digits).

(A, E, F) The group average CM bar graphs along with statistical outcomes. Error bars indicate 1 S.E.M. (A) The significant sequence type main effect is consistent with the prediction scenario shown in Fig 2.2B. (B-D) Scatter plots and correlations of CM between sequence type condition pairs. Each data point represents one participant. Filled symbols represent non-naïve participants. (E) The significant target serial position main effect is consistent with previous findings. (F) The non-significant interaction effect of sequence type and target serial position matches closer to the data pattern predicted in Fig 2.2E.

The main effect of target serial position was significant ($F_{2,30} = 9.45$, $P < 0.001$, $\eta_p^2 = 0.39$) (Fig 2.3E). The Tukey post-hoc tests of target serial positions revealed that CM significantly differed between the 4th and the 5th ($Z_{1,30} = -4.34$, $P < 0.001$), between the 4th and the 6th

($Z_{1,30} = -2.42$, $P < 0.05$), but not between the 5th and the 6th positions ($Z_{1,30} = 1.92$, $P = 0.13$). The pattern was consistent with the results of experiment 3 in Pariyadath and Eagleman (2012) that CM grows with the oddball position but eventually saturates.

Unlike the prediction of the repetition suppression hypothesis (Fig 2.2F), the interaction effect was not significant ($F_{2.65,39.82} = 1.00$, $P = 0.40$, $\eta_p^2 = 0.06$, Greenhouse-Geisser correction applied) (Fig 2.3F). Although the data pattern seemed to match the prediction of the temporal preparation hypothesis (Fig 2.2E), a planned comparison could better reveal the source of this non-significant interaction. If the temporal preparation hypothesis were really true, a later target would elicit larger CM no matter the sequence type. That is, even in the non-repeated (ordered and random) sequences, CM would be larger with a later target. A planned one-tailed t-test, averaging CM in the ordered and the random conditions, showed that this was indeed the case with the most extreme contrast (6th vs. 4th target serial position: $t_{60} = 1.88$, $P < 0.05$). Therefore, the results here favored the temporal preparation (Kim & McAuley, 2013) over the repetition suppression hypothesis (Pariyadath & Eagleman, 2012; Sadeghi et al., 2011) in explaining target serial position effect.

To our knowledge, this is the first systematic experiment directly contrasts the attention with the repetition suppression hypotheses, as well as the temporal preparation with the repetition suppression hypotheses. The results imply that both top-down attention and saliency/adaptation are necessary for explaining oddball chronostasis among digits. On top of that, temporal preparation rather than repetition suppression separately modulates the chronostasis effect.

2.4.2 Experiment 2: Orientations

One may argue that the results in Experiment 1 are specific to digits, which require more cognitive processing than basic perceptual attributes. In Experiment 2, we extended the same paradigm to stimuli varied in orientations to examine if the conclusion holds.

We obtained a similar pattern in Experiment 2. Fig 2.4 summarizes the results (N = 19) from Experiment 2. The main effect of sequence types was significant ($F_{2,36} = 3.45$, $P < 0.05$, $\eta_p^2 = 0.16$) (Fig 2.4A). Tukey post-hoc tests revealed that CM significantly differed between the repeated and the ordered conditions ($Z_{1,36} = 2.52$, $P < 0.05$), but not between the repeated and the random conditions ($Z_{1,36} = 1.97$, $P = 0.12$), or between the ordered and the random conditions ($Z_{1,36} = -0.55$, $P = 0.85$). To verify that participants performed the task with stable memory of the block-specific target in the random sequence condition, PSEs derived from the first and the second halves across all blocks were compared with a two-tailed paired t-test. The non-significant difference ($t_{18} = 0.82$, $P = 0.42$) suggested that participants had robust memory of the target. A one-tailed t-test further showed that CM in the random condition significantly differed from 0 ($t_{18} = 2.37$, $P < 0.05$). The data pattern was again consistent with the prediction in Fig 2.2B. Pearson's correlation of CM across participants between sequence types also showed similarity. The correlation was significant between the repeated and the ordered conditions ($r = 0.55$, $P < 0.05$), between the ordered and the random conditions ($r = 0.60$, $P < 0.01$), but not between the repeated and the random conditions ($r = 0.31$, $P = 0.20$) (Fig 2.4B-D). Compared with the results of Experiment 1, in general, the correlation coefficients were lower and one of them was not significant. The reason could be that specific bar orientations were not as overlearned items as digits, making the task harder and thus data pattern noisier than those in Experiment 1.

The main effect of target serial position was marginally significant ($F_{2,36} = 3.22$, $P = 0.05$, $\eta_p^2 = 0.15$) (Fig 2.4E). For the sake of comparison, the Tukey post-hoc tests of target serial positions were still performed, but one must take precaution in the interpretation. It revealed that the CM significantly differed between the 4th and the 6th ($Z_{1,36} = -2.42$, $P < 0.05$), but not between the 4th and the 5th ($Z_{1,36} = -1.88$, $P = 0.15$), or the 5th and the 6th positions ($Z_{1,36} = -0.54$, $P = 0.85$).

The interaction effect was not significant ($F_{4,72} = 0.27$, $P = 0.90$, $\eta_p^2 = 0.01$) (Fig 2.4F). To find out whether the lack of interaction was due to significant target serial position effect in the non-repeated sequences, a planned one-tailed t-test averaging CM in the ordered and the random conditions revealed that CM in the 6th was larger than that in the 4th target serial position ($t_{72} = 2.61$, $P < 0.01$). Therefore, consistent with Experiment 1, the results here also supported the temporal preparation (Kim & McAuley, 2013) over the repetition suppression hypothesis (Pariyadath & Eagleman, 2012; Sadeghi et al., 2011) in explaining target serial position effect.

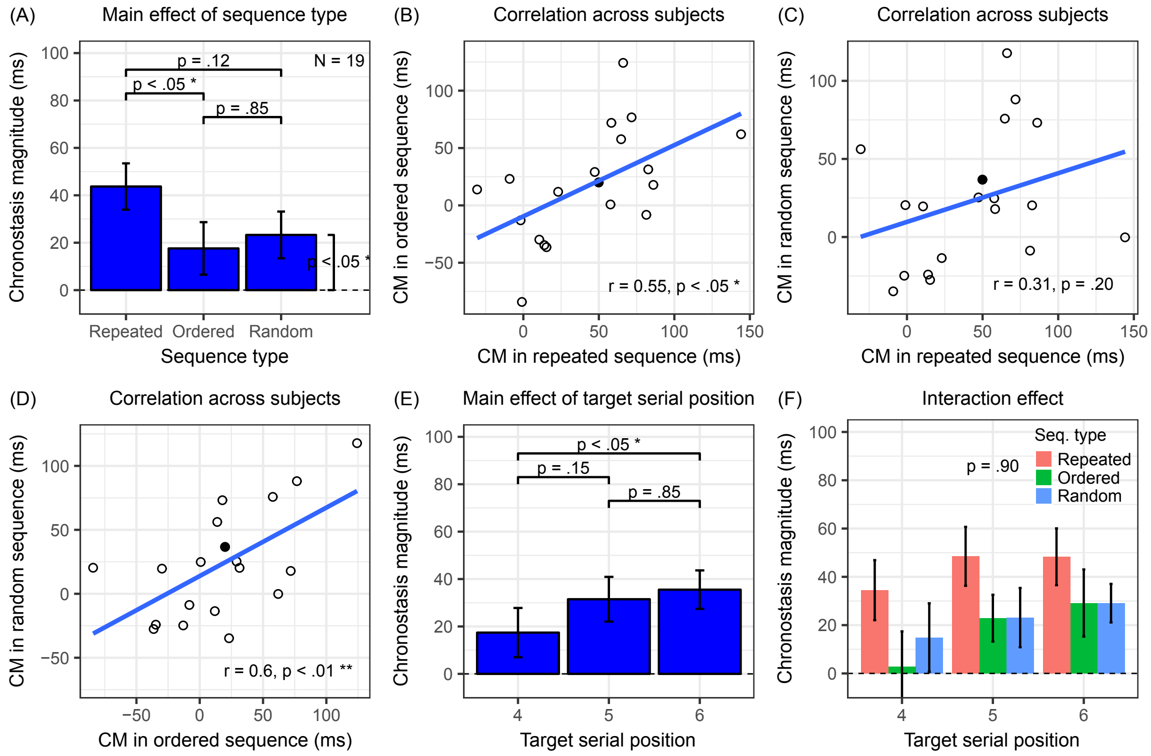

Fig 2.4. Results from Experiment 2 (orientations).

The data patterns basically replicate those in Experiment 1 (Fig 2.3). See Fig 2.3 caption for other details.

Therefore, consistent with Experiment 1, the results again imply that both top-down attention and saliency/adaptation are necessary factors of oddball chronostasis and they contribute about equally. Temporal preparation is a separate modulatory effect.

2.4.3 Experiment 3: Colors

Although Experiments 1 and 2 both arrived at the same conclusion, it is still likely that the conclusion may not be generalizable to other stimulus attributes. This motivated us to carry out an experiment with nominally isoluminant color stimuli (see Materials and Methods for details), which was, to our knowledge, never examined in the oddball chronostasis literature. Due to the difficulty of ordering colors, only the repeated and the random sequences were included. The results revealed a distinct pattern of the sequence type effect, while everything else were qualitatively similar to those in Experiments 1 and 2.

Fig 2.5 summarizes the results (N = 14) from Experiment 3. The main effect of sequence types was not significant ($F_{1,13}$= 0.07, P = 0.80, η_p^2 = 0.01) (Fig 2.5A). PSEs separately derived from the first and the second halves across all random sequence blocks were compared with a two-tailed paired t-test. The non-significant difference (t_{13} = 1.81, P = 0.09) suggested that the participants were able to perform the task with stable memory of the block-specific targets. A one-tailed t-test further showed that CM in the random condition significantly differed from 0 (t_{13} = 2.82, $P < 0.01$). The data pattern matched the prediction in Fig 2.2D instead. Therefore, it may indicate that top-down attention but not saliency/adaptation or prediction error, is a sufficient underlying factor of oddball chronostasis at least for isoluminant color stimuli. Pearson's correlation of CM across participants between the repeated and the random conditions was significant (r = 0.83, $P <$ 0.001) (Fig 2.5B). Taken together, it suggests that the common mechanism underlying the chronostasis of both sequence types is likely top-down attention.

The rest was mostly similar to Experiments 1 and 2. The main effect of target serial position was significant ($F_{2,26}$ = 4.46, $P < 0.05$, η_p^2 = 0.26) (Fig 2.5C). The Tukey post-hoc tests of target serial positions revealed that CM significantly differed between the 4th and the 6th ($Z_{1,26}$ = -2.96, $P < 0.01$), but not between the 4th and the 5th ($Z_{1,26}$ = -1.83, P = 0.16), or the 5th and the 6th positions ($Z_{1,26}$ = -1.13, P = 0.49). The interaction effect was not significant ($F_{2,26}$ = 1.72, 1144, P = 0.20, η_p^2 = 0.12) (Fig 2.5D). However, considering only the random sequence type, a planned one-tailed t-test did not reveal larger CM in the 6th than that in the

4th target serial position ($t_{26} = 0.02$, $P = 0.25$). Therefore, the results here could not directly distinguish between the temporal preparation and the repetition suppression hypothesis. As the exact isoluminant colors were harder to remember compared with the exact digits or orientations, one possible explanation was that temporal preparation might rely on unambiguous memory of the target stimulus.

It is intriguing as to why the sequence type main effect in Experiment 3 showed a disparate pattern from Experiments 1 and 2. One possibility is that color stimuli are inherently robust in saliency so as not mitigated by repetition, rendering the saliency difference between the target and the reference negligible. Another possibility is that the color stimuli differ from one another by more than one psychological dimension (hue and saturation here, unlike shape or orientation only in the previous two experiments). Analogous to the failure for conjunctive features to pop out in visual search, the oddball paradigm here can be regarded as a temporal version of visual search that is substantially harder. That is, either way, the brain may not have an advantage to spot an oddball among colors based on saliency. Future studies can 1) examine whether our conclusion in Experiments 1 and 2 holds for other stimulus dimensions, and 2) further explore the idea of saliency in temporal visual search, just as in the oddball paradigm, to fully discover the properties of spatiotemporal saliency.

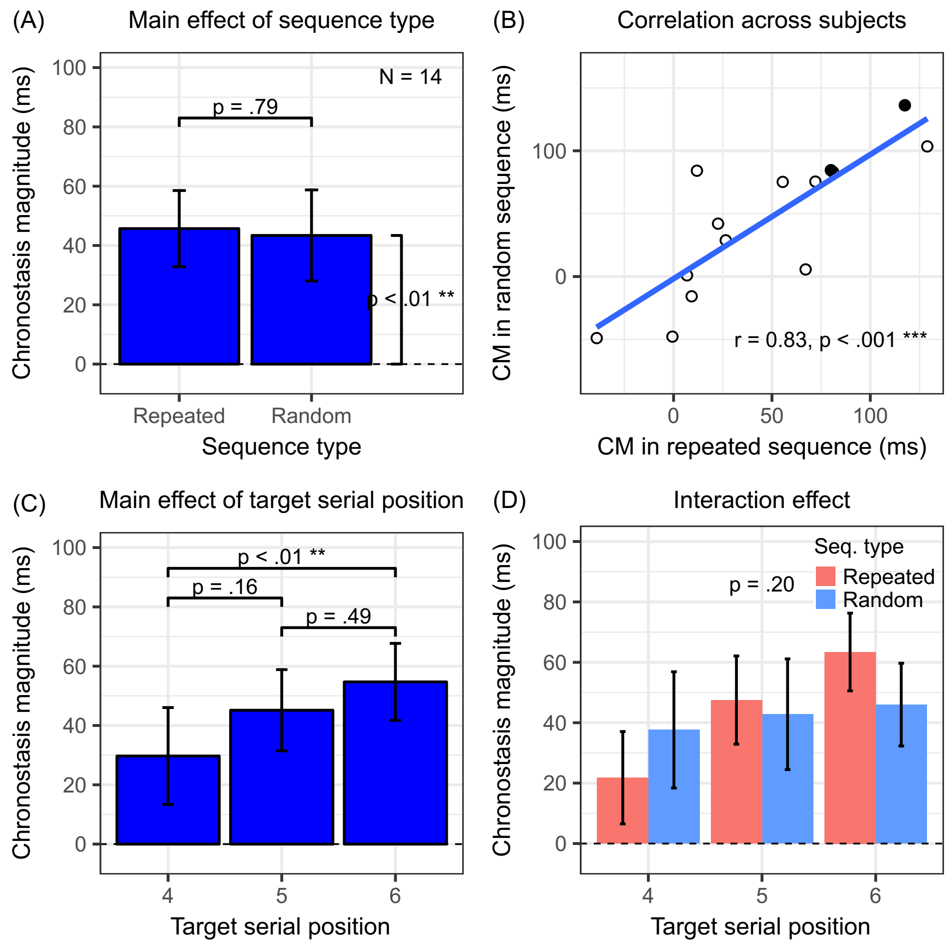

Fig 2.5. Results of Experiment 3 (colors).

There are only repeated and random sequence type conditions. (A) The non-significant sequence type main effect is consistent with the prediction scenario shown in Fig 2.2D. (B-D) Despite the stark difference in sequence type main effect from Experiments 1 and 2, other patterns remain similar to those in the first two experiments. See Fig 2.3 caption for other details.

2.5 General Discussion

2.5.1 Isolating Top-down Attention

Since the initial report of the oddball chronostasis phenomenon (Tse et al., 2004), the attention (New & Scholl, 2009; Tse et al., 2004) and the repetition suppression hypotheses (Cai, Eagleman, & Ma, 2015; Pariyadath & Eagleman, 2007, 2012; Schindel, Rowlands, & Arnold, 2011) have been separately proposed but never directly contrasted in the same experiment. Starting from theoretical analysis, we have decomposed these two hypotheses into four putative factors, and then regrouped them into three testable categories—top-down attention, saliency/adaptation, and prediction error. Empirically, our Experiments 1 and 2 together have shown that top-down attention and saliency/adaptation are the two necessary and equal contributing underlying factors of oddball chronostasis. Experiment 3 has shown that top-down attention alone is a sufficient cause. In sum, our findings suggest that top-down attention is an inherent factor underlying oddball chronostasis. The additional contribution from saliency or adaptation depends on the stimulus dimension. In other words, oddball chronostasis occurs at least partly because the oddball is a target, which has nothing to do with its being odd in the context.

2.5.2 Saliency vs. Adaptation

Among the three remaining hypotheses—saliency, adaptation, and prediction error—prediction error has been consistently ruled out both in our study and Cai et al. (2015). In our Experiments 1 and 2, there was no significant difference between the ordered and the random sequence conditions, which applied to higher-level stimuli such as digits, as well as lower-level properties such as orientations. Although in our Experiment 3, there was not an ordered condition, the insignificant difference between the repeated and the random conditions still suggested that prediction error has no role for color stimuli. In Experiment 3 of Cai et al. (2015), there was no significant difference between the expected and unexpected digit conditions either. Therefore, in this sense, the ‘surprise’ element is not a critical factor.

The evidence so far may favor the saliency over the adaptation account, but does not entirely rule out the latter one. The results of Experiment 3 can be easily explained by saliency rather than adaptation (see *Results* for details). This is supported by the discovery of Schindel et al. (see Experiment 2 of Schindel et al., 2011) that given the luminance of standards was fixed, a dimmer oddball elicited stronger chronostasis than a brighter oddball, which was against the prediction of the adaptation hypothesis. On the other hand, the results in Experiment 4 of Cai et al. (2015) showed that only when a bar is presented at the original location with the same orientation, chronostasis occurs, which is more consistent with the adaptation hypothesis. Either way, our experiment results have isolated the top-down attention factor, and narrowed down the uncertainty between attention and repetition suppression to a bottom-up source, be it saliency, adaptation, or both.

2.5.3 Origin of the Serial Position Effect

Our data also contribute to resolving a side issue—the serial position effect, where a later oddball appears to last longer in a sequence. In the literature, two separate theories were proposed. The repetition suppression hypothesis (Pariyadath & Eagleman, 2012) explains the effect by the number of same items before the target, while the temporal preparation hypothesis (Kim & McAuley, 2013) explains the effect by the accumulative anticipation of the target onset in a sequence. However, a decisive hypothesis testing has not been performed earlier. Specifically, the repetition suppression hypothesis would predict the same CM no matter the serial position if the sequence were a non-repeated one (such as ordered or random). On the other hand, the temporal preparation hypothesis predicts larger CM with later serial positions no matter the sequence type. In our study, by manipulating target serial order orthogonally to sequence type, the interaction effect was not significant across all three experiments. Specifically, non-repeated sequences still showed significant target serial position effect in Experiments 1 and 2, but not in Experiment 3. Therefore, part of the evidence in our study directly supports the temporal preparation hypothesis. It is conceivable that temporal preparation could dominate the serial position effect when the specific stimulus items (such as digits and orientations) are natural and easy to remember, while repetition suppression could prevail when the specific stimulus items are more unfamiliar to the participants. Future studies may pursue whether that is really the case. In sum, our study has systematically teased apart three separate sources of oddball chronostasis—top-down attention, saliency/adaptation, and temporal preparation.

2.5.4 Relation to Other Types of Chronostasis

Our finding that top-down attention may be an inherent component in oddball chronostasis is closely related to all types of chronostasis, such as chronostasis elicited by the first item, the last item (Rose & Summers, 1995), gaze shift (e.g., Yarrow et al., 2001), and action preparation (Hagura et al., 2012). If researchers were to identify the contributing factors underlying each type of chronostasis, it is beneficial to isolate the top-down attention part first and let it serve as a baseline, such as the role of the random sequence condition in our experiments (c.f. Birngruber, Schröter, & Ulrich, 2015).

2.5.5 Alternative Interpretations

Although the explicit prediction error component has been excluded, there may still be room for expectation or predictive coding (in the likelihood prediction sense). In a few oddball chronostasis studies, when multiple oddball types are interleaved, the higher likelihood oddball type could positively (Cai et al., 2015) or negatively (Kim & McAuley, 2013) modulate chronostasis. Similar mixed results were found in other contexts. With a two-stimulus paradigm, Ulrich, Nitschke, and Rammsayer (2006) found that a lower likelihood target elicited stronger chronostasis; by contrast, Matthews and colleagues (Matthews, 2015; Matthews & Gheorghiu, 2016) found that lower likelihood novel target induced less or no chronostasis. Since likelihood manipulation is not our main theoretical concern, we will leave this for future investigations.

Schindel and colleagues (Schindel et al., 2011) have advocated the predictive coding view to explain oddball chronostasis and proposed that attention is only drawn toward the oddball because of its lower likelihood of being presented. However, our main finding that a random sequence with 100% certainty target still elicited substantial chronostasis refutes this claim. Top-down attention may operate independently of predictive coding in perceived duration. Needless to say, our discovery resonates with how attention orienting prolongs time perception in general. For instance, exogenous (e.g., Seifried & Ulrich, 2011; Yeshurun & Marom, 2008) and endogenous (e.g., Mattes & Ulrich, 1998) spatial attention orienting, as well as exogenous and endogenous temporal attention orienting (e.g., Coull, Frith, Büchel, & Nobre, 2000; Rohenkohl, Coull, & Nobre, 2011) both lengthen time perception.

An alternative to the attention hypothesis is that the target elicits greater arousal than the other items. Initially, Pariyadath and Eagleman (2007) have demonstrated in their experiment 3 that using an emotionally salient stimulus did not make oddball chronostasis stronger. Although one may argue that it could be due to ceiling effect, in light of the findings of Cai et al. (2015) and our Experiments 1 and 2, the 'surprise' element (ordered vs. random, see green bars vs. blue bars in Figs 2.3F and 2.4F), which presumably would also have elevated arousal, did not in turn modulate CM. Therefore, the arousal hypothesis is overall less likely.

2.5.6 Neurophysiological and Computational Implications

Resolving the debate over attention vs. repetition suppression and over temporal preparation vs. repetition suppression (see all likely scenarios in Fig 2.2) is critical to identifying the roles of underlying neural mechanisms. Qualitatively, our study has experimentally dissociated three separate factors that give rise to oddball chronostasis— top-down attention, saliency/adaptation, and temporal preparation. Quantitatively, the relative contribution ratio of top-down attention to saliency/adaptation is essential to computational modeling of perceived duration. We have demonstrated that it could be close to 1:1 or 1:0 depending on the stimulus dimension (digits, orientations, or color). The experimental design can thus be utilized in future neural imaging studies to pin down the neural correlates of each source. Since many flavors of neural models have been proposed (for an overview, see Ivry & Schlerf, 2008), it remains to be seen whether these three top-down and bottom-up sources of human duration perception modulators converge onto the same network node to determine perceived duration. If this were the case, the sensory cortex neural response amplitude hypothesis advocated by Eagleman and colleagues (Cai et al., 2015; Eagleman & Pariyadath, 2009; Pariyadath & Eagleman, 2012; Sadeghi et al., 2011) might be one interesting possibility. If not, a core timing network which consists of the supplementary motor area and the basal ganglia along with other context-dependent nodes (Merchant, Harrington, & Meck, 2013) could be separately regulated by these three disparate factors. The answers await future investigations.

2.6 Conclusions

1. This is the first study that directly contrasts the attention with the repetition suppression theories, and the temporal preparation with the repetition suppression accounts. The discoveries are crucial to understanding the mechanisms underlying how time is perceived in a context.

2. Our experiments tested three categories of theoretical components to resolve the controversy between the attention (New & Scholl, 2009; Tse et al., 2004) and the repetition suppression theories (Cai, Eagleman, & Ma, 2015; Pariyadath & Eagleman, 2007, 2012; Schindel, Rowlands, & Arnold, 2011) of oddball chronostasis: top-down attention, saliency/adaptation, and prediction error.

3. Results suggest that top-down attention is sometimes sufficient (to isoluminant colors) and the other sometimes necessary (to digits and orientations) to explain oddball chronostasis. In the latter case, it explains about half of the effect; saliency/adaptation explains the other half. Prediction error does not play a critical role.

4. Between the temporal preparation (Kim & McAuley, 2013) and the repetition suppression hypothesis (Pariyadath & Eagleman, 2012; Sadeghi et al., 2011), the data with digits and orientations favor the former because non-repeated (ordered or

random) sequences still exhibit target serial position effects. In this case, prior repetitions are not crucial to render a later target appear lasting longer.

5. Therefore, oddball chronostasis has two important underlying contributors unrelated to event oddness or unexpectedness—top-down attention and temporal preparation; sometimes bottom-up saliency/adaptation co-contributes.

2.7 Acknowledgements

This work was supported by the National Science Foundation (NSF BCS-1439372) and Japan Science and Technology Agency CREST to Shinsuke Shimojo (principal investigator). We thank Daw-An Wu for his input on refining the visual stimuli and comments on the manuscript.

The authors declare that there are no commercial relationships.

Chapter III

INTERNAL DURATION UNCERTAINTY DILATES SUBJECTIVE TIME

3.1 Abstract

Everybody knows roughly how long one second lasts, but when is this internal standard calibrated? Here we investigated a simple yet not well understood contextual effect on duration perception, termed debut chronostasis, which refers to the phenomenon that the first item in a repeating visual item sequence appears to last longer in duration, in contrast to the similar relative duration between the second and the third items. Earlier studies explained the phenomenon either by increased attention towards the first item or relatively suppressed neural encoding for the ensuing repeated items. However, two other possibilities were overlooked. First, assigning one item as the target and another as the reference may create a cognitive bias (instruction effect). Second, the item that varies in duration across trials may induce uncertainty in the internal duration template. The extra effort paid to calibrate the internal duration template could lead to subjective time distortion (uncertainty effect). In Experiment 1, we examined three comparison pairs (variable target vs. constant reference): first vs. second (1 vs. 2), 2 vs. 1, and 2 vs. 3. As expected, 1 vs. 2 produced debut chronostasis and 2 vs. 3 did not result to relative duration difference. By contrast, in the 2 vs. 1 condition, debut chronostasis was largely reduced, if not entirely disappeared. Experiment 2 kept the same explicit instruction regarding which item was the target/reference, but the reference instead of the target varied across trials (comparison pairs became constant target vs. variable reference). Compared with Experiment 1, the results showed mostly the uncertainty effect but not the instruction effect in the 1 vs. 2 and 2 vs. 1 conditions. The relative duration in the 2 vs. 3 condition was still unaffected. Therefore, the overall discoveries imply that the internal duration template is calibrated once per trial and disrupted when the first item has variable duration. Future chronostasis studies shall take this internal duration uncertainty effect into account, especially when the relative subjective duration measurement happens to

involve a variable first item, where it was indeed the case in many previously published chronostasis studies.

3.2 Introduction

Subsecond duration perception is surprisingly prone to distortion in different stimulus temporal contexts. The extent to how relative rather than absolute duration judgments are provide important clues to how exactly durations are perceived. For instance, in a repeating visual item sequence, Rose and Summers (1995) discovered that the first item and the last item appeared to last longer (*debut* and *finale chronostasis*). Tse, Intriligator, Rivest, and Cavanagh (2004) found that among repeating identical items, an occasional odd item appeared to last longer (*oddball chronostasis*). Complementarily, Pariyadath and Eagleman (2008) showed that repeated items appeared subjectively shorter. Kim and McAuley (2013) suggested that a later repeating item in a sequence could be perceived as longer because the build-up of anticipation could hasten its apparent onset. Lin and Shimojo (2017) revealed that in a random item sequence, a designated target item also appeared to last longer in duration.

In this study, we aim to push forward the theoretical understanding of debut chronostasis, which is arguably one of the simplest temporal context effects, where identical items were repeated. Since its initial discovery by Rose and Summers (1995), they explained the phenomenon by increased attention specifically elicited by the first item in a sequence. With a sequential four-item paradigm, they found that the first item could appear longer than the second one by 50% in duration in the extreme case. By contrast, the second and the third items appeared to have about the same subjective duration. Therefore, it is not just the temporal-order error effect in two-item duration discrimination experiments where the first item does not always appear to have longer duration (c.f. Allan, 1979; Hellström, 1979). They also ruled out arousal as an account because stimulus brightness did not significantly modulate the effect. Later Eagleman and colleagues challenged the attention account and proposed the repetition suppression hypothesis to explain the phenomenon (Cai, Eagleman, & Ma, 2015; Pariyadath & Eagleman, 2007). Using digits as stimuli, they found that when the digits following the first are random disparate ones, debut chronostasis is nullified. Hence, they argued that attention is not the key mechanism.

Although repetition suppression is a likely explanation, here we instead examined two fundamental factors that were overlooked in quite a few types of chronostasis studies, including debut chronostasis (Cai, Eagleman, & Ma; Rose & Summers, 1995; Pariyadath & Eagleman, 2007), saccadic chronostasis (e.g., Yarrow et al., 2001), and oddball chronostasis (e.g., Tse, Intriligator, Rivest, & Cavanagh, 2004). In all these previous studies, the target duration being measured coincided with the item that varied in duration across trials. First, it is likely that the instruction assignment of one item as target and some others as the reference introduces cognitive bias (instruction effect). Second, it is also possible that the item varies in duration across trials poses uncertainty to the duration judgment and lengthens the apparent duration by creating extra mental effort (uncertainty effect).

Findings from several earlier studies provide hints to these two specific hypotheses. For the instruction effect hypothesis, in our earlier oddball chronostasis studies (Lin & Shimojo, 2017), we have isolated a top-down attention component by showing that a target item among other random items appear to last longer. Therefore, being an explicit cognitive target itself may induce chronostasis.

As for the uncertainty effect hypothesis, debut chronostasis may be indirectly related to a virtual (or implicit) standard effect (Morgan, Watamaniuk, & McKee, 2000; Nachmias, 2006). Morgan and colleagues (2000) discovered that threshold estimates with method of single stimuli are nearly identical to those with method of constant stimuli while presenting standard first and comparison later (constant first, variable later, or simply constant-variable condition). Nachmias (2006) further found that discrimination sensitivity is higher in the constant-variable than in the variable-constant condition no matter whether the block type is mixed or alone. This pattern of discrimination sensitivity difference not only applies to visual discrimination (Morgan, Watamaniuk, & McKee, 2000; Nachmias, 2006) but also to duration discrimination (Bausenhart, Dyjas, & Ulrich, 2015; Dyjas, Bausenhart, & Ulrich, 2012; Hellström and Rammsayer, 2015; Lapid, Ulrich, & Rammsayer, 2008; Ulrich, 2010; Ulrich & Vorberg, 2009). Although these studies with the classic two-item discrimination paradigm did not specifically find that the variable item tend to appear subjectively longer than the constant item, there is a possibility that in debut chronostasis studies where the standards are presented multiple times per trial (Cai, Eagleman, & Ma; Rose & Summers, 1995; Pariyadath & Eagleman, 2007), the brain relies more on the implicit duration reference more. Accordingly, when uncertainty is introduced to the implicit duration reference through variable items, over-estimation may occur. If this were the case, then debut chronostasis could be in fact *uncertainty chronostasis*.

To test these two ideas, in Experiment 1, we kept Rose and Summers' original first item vs. second item (1 vs. 2) and second item vs. third item (2 vs. 3) conditions, and introduced a new second item vs. first item (2 vs. 1) condition. In each comparison pair, the former item was the explicit "target" and the latter was the "reference" by instruction; the target was always the item varied in duration across trials. Indeed, we did discover that debut chronostasis was nullified, but not entirely reversed in the 2 vs. 1 condition. In Experiment 2, in order to determine whether the main result was due to the instruction effect regarding which item was the target or reference, or to the uncertainty effect regarding which item varied across trials, the instructions remained the same. Without explicitly informing the participants, the reference item varied in duration across trials instead. The results revealed that duration uncertainty was the major factor governing debut chronostasis. Theoretical implications will be discussed in the end.

3.3 Materials and Methods

3.3.1 Participants

The experiment protocols were approved by the institutional review board of California Institute of Technology (Caltech). The participants were drawn from the Caltech brain science subject pool, which mainly consisted of Caltech and Pasadena City of College students. In Experiment 1, there were 12 observers (6 female; 9 naïve; 20-60 years; M = 30.9; SD = 11.1). In Experiment 2, there were 14 observers (6 female; 13 naïve; 19-51 years; M = 28.5; SD = 8.8). Two observers (one naïve) also participated in Experiment 1 before Experiment 2. All participants provided written informed consent before the experiments. The naïve participants were paid for their cooperation.

3.3.2 Apparatus

The stimuli were presented using a Lacie Electron 22 Blue IV monitor in both experiments. The screen resolution was set at 800 (H) x 600 (V) with frame rate 120Hz. The viewing distance was 70cm. The stimuli presentation code was written in Python with PsychoPy toolbox (Peirce, 2007) under Mac OS X. To ensure that the timing was precise, a preemptive setting was adopted to override other background processes.

3.3.3 Design and Predictions

In Experiment 1, there were three within-subject comparison pair conditions: T1R2, T2R1, and T2R3. They read as target 1-reference 2, target 2-reference 1, and target 2-reference 3, respectively. In each condition, there were exactly four items presented sequentially (more details in *4.3.5 Procedure*). The former digit represented which item was the target, which the participants were informed of, while the latter digit represented which item was the reference. However, the participants were not explicitly told that the target had variable duration across trials (in typical psychophysics literature, this is often called the *test*) while the reference had constant and the same duration as other irrelevant items (the *standard*). Participants' task was to judge whether the target lasted shorter or longer than the reference. For example, in the T2R1 condition, participants judged whether the second item lasted shorter or longer than the first one. As Rose and Summers (1995) reported that in the T1R2 condition, the first item appeared longer than the second item in duration (debut chronostasis), and in the T2R3 condition, the subjective duration of the second and the third items were about the same. We expect similar results or in the T2R3 condition the second item may be perceived as slightly longer in duration than the third if the repetition suppression hypothesis were true. In the novel T2R1 condition, if debut chronostasis were solely due repetition suppression, then the outcome should be the same as in the T1R2 condition; otherwise, any significant deviation from the T1R2 condition could suggest previously overlooked underlying mechanisms. More specifically, if debut chronostasis disappeared, or even reversed (the second item perceived as longer instead), then it would suggest that the instruction effect or the uncertainty effect hypothesis is true.

Indeed, we did find significant difference between the T1R2 and the T2R1 conditions from Experiment 1. In Experiment 2, everything was the same as in Experiment 1 except that as opposed to Experiment 1, the target had constant (the *standard*) while the reference had variable duration across trials (the *test*). The participants were not explicitly informed of this setting either. If the data pattern in Experiment 2 were exactly the same as in Experiment 1, then the nature of the significant difference between the T1R2 and the T2R1 conditions could be top-down attention effect as manipulated by explicit instructions regarding which item were the target. On the contrary, if the outcome in the T1R2 and the T2R1 conditions flipped, then it would be more likely an instance of uncertainty effect, which is potentially implicit. If the uncertainty effect underlay the T2R3 conditions, the outcome of the T2R3 condition in Experiments 1 and 2 would be opposite because of the swap of the test and the standard.

In both experiments, the dependent variable was relative apparent duration (RAD) between the earlier and the later item in each comparison pair. The more positive RAD was, the longer the earlier item appeared relative to the latter item. In other words, RADs in the T1R2 and the T2R1 conditions both meant the magnitude of debut chronostasis. RAD in the T2R3 condition meant the magnitude of how much the second item was perceived longer than the third item. The calculation of RAD will be described in detail in the later subsections. The RADs were analyzed with a one-way repeated measures analysis of variance (ANOVA).

3.3.4 Stimuli

All visual stimuli were presented at the center of the screen where there was a constant red fixation point spanning 0.1° (H) x 0.1° (V) visual angle at the center of the screen. The background was black. In both experiments, the stimuli were white squares each spanning 4.0° (H) x 4.0° (V) visual angle.

3.3.5 Procedure

The participants' task was to discriminate the duration between the target item and its reference. They were forced to make their best guess and to choose either target perceived "shorter" or "longer" than the reference using one of two keys on the computer keyboard.

In each trial, 4 items were presented one at a time. The participants were instructed to respond only after all items had been presented. This long gap between the target item presentation and the response helped avoid chronostasis induced by action preparation (e.g., Hagura et al., 2012). Duration of all items except the test (was the explicitly defined target in Experiment 1 and reference in Experiment 2) was fixed at 600 ms. Centered around that standard duration, the target duration varied in 8 levels from 250 to 950 ms in 100 ms steps. Each inter-stimulus interval (ISI) was random, chosen from a uniform distribution between 250 and 500 ms. Each inter-trial interval (ITI) was random, chosen from a uniform distribution between 700 and 1100 ms.

Every participant was tested in 3 sessions, where each session comprised a practice block and 5 experimental blocks of a given comparison pair condition. The order of comparison pair conditions was random per participant. A session typically took about 18 minutes. Each session had a sequence type specific experimental instruction. In the practice block, there were 16 trials comprising only the more extreme target durations (250, 350, 850, and 950 ms). These practice trials were excluded from analysis. In each experiment block, all 8 target durations were repeated 4 times, resulting to 32 trials. The order of the trials were randomly shuffled within each block. Before each block, an instruction screen indicated the chance to take a short break.

3.3.6 Psychometric Function and Relative Apparent Duration

In each comparison pair condition, the probability of a participant reporting the target as subjectively longer than the reference were calculated. A cumulative Gaussian distribution was fitted to those data to estimate psychometric functions. The point of subjective equality (PSE) of each condition was the corresponding physical duration when the probability was 0.5 on the psychometric function. In experiment 1, targets (see the definitions in *4.3.3 Design and Prediction*) were varied in duration across trials; RADs were defined as standard duration—PSE in the T1R2 and the T2R3 conditions, and PSE—standard duration in the T2R1 condition. As explained earlier in section 4.3.3, the more positive RAD is, the longer an earlier item appeared relative to its next item. For example, in the T1R2 condition, if PSE of the target (the first item) were 500 ms, then RAD were 600 - 500 = 100 ms, indicating that the earlier (the first) item appeared subjectively longer than the later (the second) item by 100 ms. In experiment 2, references were varied in duration across trials instead. Therefore, the sign of RADs flipped. The definitions became PSE—standard duration in the T1R2 and the T2R3 conditions, and standard duration—PSE in the T2R1 condition. For example, in the T1R2 condition, if PSE of the reference (the second item) were 700 ms, then RAD were 700 - 600 = 100 ms, indicating that the earlier (the first) item appeared subjectively longer than the later (the second) item by 100 ms.

3.4 Results

3.4.1 Experiment 1: Varying Target Duration

A one-way repeated measures ANOVA was performed on the RADs across three comparison pair conditions. Fig 3.1A summarizes the results (N = 12) from Experiment 1. The main effect of comparison pairs was significant ($F_{2,22} = 9.83$, $P < 0.001$, $\eta_p^2 = 0.47$). Tukey post-hoc tests revealed that RADs significantly differed between the T1R2 and the T2R1 conditions ($Z_{1,22} = 2.91$, $P < 0.05$), between the T1R2 and the T2R3 conditions ($Z_{1,22}$

= 4.35, $P < 0.001$), but not between the T2R1 and the T2R3 conditions ($Z_{1,22} = 1.45$, $P = 0.32$). The surprising finding was that the RAD in the T1R2 was greater than that in the T2R1 condition. It implies that either the uncertainty effect (which item is variable across trials) or the instruction effect (which item is the explicit target) plays an important role.

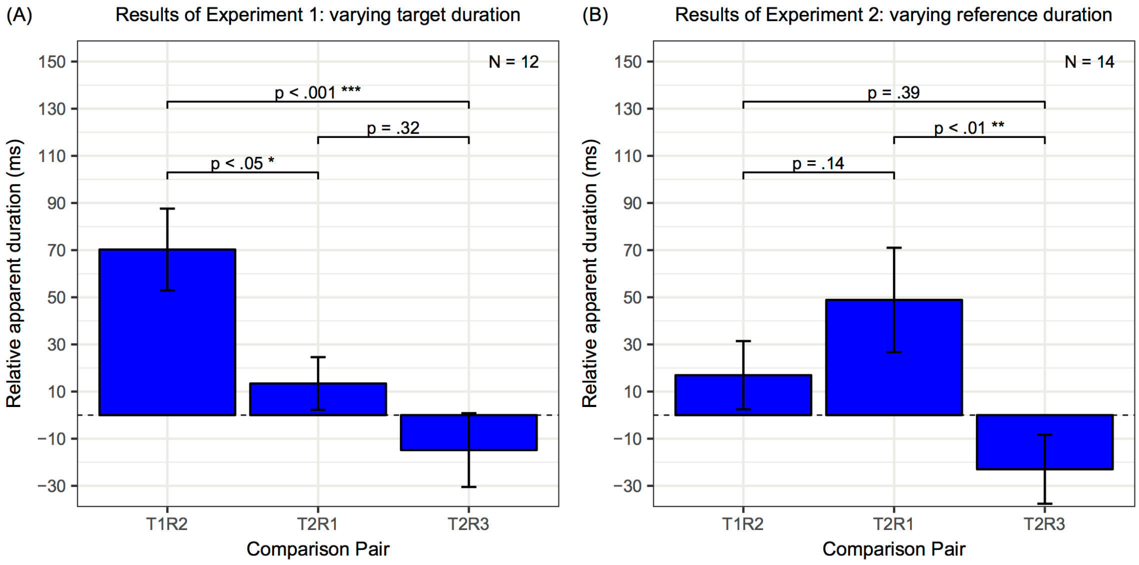

Fig 3.1. Results from Experiments 1 and 2.

Relative apparent duration in different comparison pair conditions. Positive direction indicates that the earlier item in a pair is judged subjectively longer than the later item. (A) In Experiment 1, the target was the item varied in duration across trials. Debut chronostasis occurred in the T1R2 but not the T2R1 condition (also see text for t-test results against 0). (B) In Experiment 2, the reference was the item varied in duration. The pattern of T1R2 vs. T2R1 is almost reversed. Across these two experiments, the data pattern suggests that the uncertainty effect substantially modulates perceived time specifically to the first two items.

Post-hoc two-tailed t-tests were performed on the RAD in each condition to determine whether RAD was different from 0. With Bonferroni correction, the alpha values for these tests were 0.05/3 ~= 0.017. It turned out that RAD was different from 0 in the T1R2 condition

($t_{11} = 4.05$, $P < 0.017$), but not in the T2R1 ($t_{11} = 1.20$, $P = 0.25$) or the T2R3 ($t_{11} = -0.95$, $P = 0.36$) conditions. The significant effect in the T1R2 condition and the insignificant effect in the T2R3 condition were consistent with the patterns in the debut chronostasis literature (Cai, Eagleman, & Ma, 2015; Pariyadath & Eagleman, 2007; Rose & Summers, 1995). By contrast, our result that debut chronostasis became nullified in the T2R1 condition was novel discovery.

3.4.2 Experiment 2: Varying Reference Duration

As the novel finding in Experiment 1 confounded the explicit instruction and the uncertainty effects, we carried out Experiment 2. In Experiment 2, the only difference was that the reference became the item varied in duration across trials. All the other details of experimental designs, procedures, and instruction to the participants were the same. The participants were not explicitly informed that only one item varied in duration across trials and that item was the reference in this experiment. If the uncertainty effect were the only underlying factor, then debut chronostasis should occur only in the T2R1 but not the T1R2 condition in this experiment. If the repetition suppression hypothesis were true, then debut chronostasis should be the same in the T1R2 and the T2R1 conditions because the average variable (test) duration is the same as the constant (standard) duration. As for the T2R3 condition, since it was not significant in Experiment 1, if repetition suppression were true, the same weak modulation would still predict nonsignificant effect. If the uncertainty effect were specific to the first two items as in Experiment 1, the same null effect were expected here in Experiment 2. A one-way repeated measures ANOVA was performed on the RADs across three comparison pair conditions. Fig 3.1B summarizes the results (N = 14) from Experiment 2. The main effect of comparison pairs was significant ($F_{1.36,17.70} = 5.85$, $P < 0.05$, $\eta_p^2 = 0.31$, Greenhouse-Geisser correction applied). Tukey post-hoc tests revealed that RADs significantly differed between the between the T2R1 and the T2R3 conditions ($Z_{1,26} = 3.39$, $P < 0.01$), but not between T1R2 and the T2R1 conditions ($Z_{1,26} = -2.09$, $P = 0.09$), or between the T1R2 and the T2R3 conditions ($Z_{1,26} = 1.30$, $P = 0.39$). Although the RADs did not differ between the T1R2 and T2R1 conditions, overall the results here suggest that the data pattern in Experiment 1 was at least partly, if not primarily, due to the item varied in duration across trials.

Post-hoc two-tailed t-tests were performed on the RAD in each condition to determine whether RAD was different from 0. It turned out that RAD was different from 0 in the T2R1 condition ($t_{13} = 2.75$, $P < 0.017$), but not in the T1R2 ($t_{13} = 1.03$, $P = 0.32$) or the T2R3 ($t_{13} = -1.31$, $P = 0.21$) conditions. The significant effect in the T2R1 instead of the T1R2 condition suggests that instruction on which item was the target or reference did not play a critical role. Only when the first item was varied in duration across trials, debut chronostasis emerged.

This debut chronostasis nullification by switching the order of the target and the standard led us to ask whether the results were also applicable to the comparison between the second and the third item. In the T2R3 condition of Experiment 1, the second item was the one varied in duration across trials; in the T2R3 condition of Experiment 2, the third item was the one varied. An unequal sample two-tailed t-test, however, did not reveal significant difference of this condition between the two experiments ($t_{23.7} = 0.23$, $P = 0.81$). This suggests that the uncertainty effect was specific to the first two items in the sequence. Although this could possibly be reasoned as plateaued repetition suppression effect, repetition suppression could not explain why debut chronostasis only occured in the T2R1 but not the T1R2 condition here, given that the average test duration is the same as the standard duration.

3.5 General Discussion

3.5.1 Main Findings and Interpretations

We have discovered that the uncertainty effect could substantially affect judged duration between the first and the second item in the four-item sequence. Besides confirming the basic results in the literature, such as the presence of debut chronostasis whenever the first item was the test that varied in duration across trials (Cai, Eagleman, & Ma, 2015;

Pariyadath & Eagleman, 2007; Rose & Summers, 1995), and the absence of RAD between the second item and the third item (Rose & Summers, 1995), Experiment 1 revealed that debut chronostasis became absent whenever the second item was the test item that varied. Experiment 2 further clarified that the main finding was due to the uncertainty effect rather than the explicit instruction effect on which item was the target or the reference. The unexpected result that the RADs were significantly different between these two conditions in Experiment 1 actually highlights an important overlooked component of duration perception.

Our results here have ruled out three simple explanations in addition to the instruction effect hypothesis. First, if debut chronostasis were due to response bias, such as the preference to choose "longer" over "shorter," the outcomes in the T1R2 conditions across both experiments would have been the same. However, this was not the case in our results. Second, if debut chronostasis were just another instance of time-order error (TOE, after Fechner, 1860/1966) in duration comparison where the sequential order biases the relative perceived duration (Hellström, 1977), the RAD would share similar biases (either positive or negative) in both the T1R2 and T2R3 conditions (Allan, 1977). However, both our results confirmed the report of Rose and Summers (1995) that the second and the third item do not have significantly different relative duration. Third, the main results were against a simple attention account that the first visual flash in a train will automatically attract spatial attention (Jonides, 1981; Hoffman et al., 1983; Yantis and Jonides, 1984).

The original repetition suppression hypothesis (Pariyadath & Eagleman, 2007; Cai, Eagleman, & Ma, 2015) may not explain our results either. Specifically, Eagleman and Pariyadath (2009) hypothesized that the sensory neural response amplitude could directly code perceived duration. Therefore, given that all items had identical visual attributes and the average test duration equaled the standard duration, the repetition suppression hypothesis would predict the same RAD in the T1R2 and the T2R1 conditions, which was not supported by our data. As for the nonsignificant RAD in the T2R3 condition of both experiments, it may not be compatible with the repetition suppression account either.

Sadeghi, Pariyadath, Apte, Eagleman, and Cook (2011) showed by fMRI that repetition suppression in the middle temporal visual cortex lasted until at least 15 items for repeated items and the trend was quite linear. Thus, the sudden floor effect between the second and the third items looks more like against the neural data. Still, there is a possibility that other neural correlates capturing the RAD patterns may be found in the future. Therefore, the repetition suppression hypothesis cannot be entirely ruled out.

More parsimoniously, our findings may be explained by how uncertain the internal duration standard (template) is. In both Experiments 1 and 2, debut chronostasis only occurred when the first item varied in duration. This indicates that the stability of the internal duration template might decay substantially after about 1 second (assume that response time was roughly half a second and after that ITI was 700-1100 ms), but may still preserve to some extent after the ISI, which was 250~500 ms. Therefore, the first item in each trial is the most informative one for refreshing the internal template. This explains why debut chronostasis was evident in the T1R2 condition of Experiment 1 and T2R1 condition of Experiment 2 but not in all the other conditions—only in these two conditions, the first item varied in duration and thus contributed less in stabilizing the internal duration template. Although it is not yet clear why uncertainty must lead to subjective time expansion rather than contraction, this suggests that debut chronostasis could be primarily uncertainty chronostasis. An educated guess is that a variable first item may draw elevated implicit attention so as to accelerate the internal clock speed (e.g., Gibbon, Church, & Meck, 1984).

3.5.2 Relations to The Classic Two-Item Paradigm

Our main finding that debut chronostasis arising mostly from the duration uncertainty of the first item may not be directly generalized to the classic two-item duration discrimination paradigm for the following reasons. First, a two-item paradigm may potentially confound finale chronostasis (apparently longer duration of the last item, reported by Rose and Summers, 1995) or action preparation chronostasis (e.g., Hagura et al., 2012). Second, most studies using a two-item paradigm kept the ISI fixed, which could provide extra cues about the onset of the next item. For example, McAuley & Fromboluti (2014) showed that entrained rhythm can substantially affect perceived duration of an item that deviates from the rhythm. Third, in previous two-item studies, both time-order error (TOE) and the presentation order effect (variable or constant item first) showed mixed (positive, insignificant, and negative) results on relative subjective duration (e.g., Allan, 1977; Bausenhart, Dyjas, & Ulrich, 2015; Hellström, 1977; Hellström & Rammsayer, 2015; Jamieson and Petrusic, 1975). Although the variability across studies (Allan, 1977) can be fitted by a linear sensation weighting model (Hellström, 1979), how many underlying mechanisms are involved is still unclear. Future studies may directly compare the results obtained with two-item and four-item paradigms to bridge the knowledge gap.

3.5.3 Relations to Other Types of Chronostasis

Our discovery on debut chronostasis suggests that internal duration uncertainty expands subjective time. In quite a few duration distortion studies (e.g., Cai, Eagleman, & Ma; Rose & Summers, 1995; Pariyadath & Eagleman, 2007; Tse, Intriligator, Rivest, & Cavanagh, 2004; Yarrow et al., 2001), researchers focused on the PSE of the target in question but did not pay attention to this specific aspect of experimental design, and thus did not attempt to exchange the test-standard order. In other words, the duration uncertainty effect may at least partly underlie, if not potentially inflate, many of the earlier discovered subjective time expansion phenomena. Thus, future studies may utilize our discovery for a more complete understanding of the foundation of duration perception. Here we have at least shown that when all items were identical, the duration variability of the first item critically determined perceived duration.

In the context of oddball chronostasis, this test-standard order effect has never been examined. Recently, Lin and Shimojo (2017) used a random item sequence and instructed the participants to look for a specific target item and compare the target's duration against its previous one. They found that simply being a target expands its apparent duration, and explained the effect by top-down attention. Although in that study, the target was never the first item, still the target coincided with the item varied in duration across trials. It would be interesting to examine whether that was partly due to the duration uncertainty effect.

3.6 Acknowledgements

This work was supported by the National Science Foundation (NSF BCS-1439372) and Japan Science and Technology Agency CREST to Shinsuke Shimojo (principal investigator).

The authors declare that there are no commercial relationships.

Chapter IV

DEBUT CHRONOSTASIS: THE INTRA- AND SUPRA-MODAL ASPECTS OF TIME PERCEPTION MECHANISMS

4.1 Abstract

In a train of multiple visual flashes, the first item appears to expand in time relative to the second one (debut chronostasis) when the measurement method involves a variable first item and a constant second item, but not vice versa. In Chapter III, we have reasoned that debut chronostasis may originate from uncertainty of the internal duration template. In this chapter, as an attempt to understand the properties of the internal duration template, we challenged the previous finding that debut chronostasis only occurs in the visual modality by testing the auditory modality and inter-modal conditions. In Experiment 1, with a four-item paradigm, the first and the second items were among four conditions: V-V (first visual-second visual), A-A (auditory, auditory), V-A, and A-V. The physical duration of the first item varied across trials. Participants' task was to judge whether the first item lasted shorter or longer than the second one. In Experiment 2, the only difference was that the second item varied in duration instead. There were three novel findings. First, auditory debut chronostasis had similar debut chronostasis magnitude (DCM) as the visual case. Second, average DCM was higher in intra- (V-V and A-A) than in inter-modal (V-A and A-V) conditions in both experiments. Third, as shown in our earlier finding (Chapter III), reversing the variable and constant items from Experiment 1 to 2 could at least greatly reduce DCM in the V-V condition, again indicating that uncertainty dilates duration. Surprisingly, this magnitude reduction applied to all four conditions by similar amounts. The second and the third findings appear to be linearly additive effects. In sum, the higher average DCM in the intra- than in the inter-modal conditions suggest a presence of "within-modal" clock, whereas the yet-significant (though reduced) DCM in inter-modal condition, as well as the similar reduction across the intra- and inter-modal conditions, together imply a supra-modal mechanism contributing to time

expansion. Therefore, both within- and supra-modal mechanisms may underlie debut chronostasis.

4.2 Introduction

To what extent time perception is dependent on or independent of primary senses is still an open issue under investigation. On the one hand, every primary sense as well as action has a temporal aspect. On the other hand, there could be specialized but metamodal neural mechanisms for time perception (for a review, see Ivry & Schlerf, 2008). In this study, we aim to address this issue by examining whether a previously reported time illusion, debut chronostasis (Cai, Eagleman, & Ma, 2015; Pariyadath & Eagleman, 2007; Rose & Summers, 1995; see also Chapter III), is a time illusion in the visual domain only (Rose & Summers, 1995), or also occurs in the auditory or even cross-modal situations.

The subjective time expansion illusion that the first item in a multiple identical item sequence, is a contextual effect on time perception among other related phenomena such as that the last item (Rose & Summers, 1995), or an odd item (Tse, Intriligator, Rivest, & Cavanagh, 2004) in a multiple item appears to last longer than the others. For simplicity, we will refer to this phenomenon as debut chronostasis following other researchers' usage of the term 'chronostasis' as a shorthand of subjective time expansion (Hodinott-Hill et al., 2002; Yarrow, 2010; Yarrow & Rothwell, 2003; Yarrow et al., 2001).

The main factor that leads to debut chronostasis is likely the uncertainty in internal duration template (see Chapter III). In classic two-item discrimination tasks, both vision (Nachmias, 2006) and time perception researchers (Bausenhart, Dyjas, & Ulrich, 2015; Dyjas, Bausenhart, & Ulrich, 2012; Hellström and Rammsayer, 2015; Lapid, Ulrich, & Rammsayer, 2008; Ulrich, 2010; Ulrich & Vorberg, 2009) have found a standard position effect on discrimination sensitivity, where the standard (constant duration) first, test (variable duration) later condition has higher discriminability than the test first, standard later condition. Morgan et al. (2000) and Nachmias (2006) first pointed out this is likely because human observers by default maintain an implicit virtual standard based on recent stimulus history. Inspired by these earlier discoveries of standard position effect on discrimination sensitivity, we further found that standard position effect could modulate perceived duration. Only when the first item varied in duration, debut chronostasis occurred. The internal duration template may decay rather quickly after the inter-trial interval but persist through the inter-stimulus intervals. Therefore, only the uncertainty in the first item induces debut chronostasis. The way uncertainty expands subjective time might be through elevated implicit attention that accelerates the internal clock speed (Chapter III).

In this study, we were interested in exploring whether the internal duration template exclusively exists in the visual modality, as Rose and Summers (1995) did not find auditory debut chronostasis. We hypothesize that debut chronostasis actually exists in the auditory domain. In Rose and Summers (1995), the inter-stimulus interval (ISI) was fixed. With ISI fixed, repetitive items with the same standard duration could entrain rhythmic perception and thus attention to onset and offset timings (e.g., McAuley & Fromboluti, 2014). Given that the auditory sense has better temporal acuity than the visual modality (e.g. Rammsayer, Borter, and Troche, 2015), it is likely that more accurate detection of item onsets and offsets could easily correct the illusion of auditory debut chronostasis. Thus, we hypothesize that when ISI is random instead of fixed, auditory debut chronostasis will appear. If it turned out that auditory debut chronostasis exists, then two upcoming questions are whether auditory debut chronostasis has similar magnitude as visual debut chronostasis, and whether debut chronostasis could occur even intermodally.

In Experiment 1, we examined whether debut chronostasis occurred in V-V (first visual, second visual), A-A (first auditory, second auditory), V-A, and A-V conditions. The first item varied in duration across trials. Thus, as expected from Chapter III, debut chronostasis would at least occur in the V-V condition. Whether debut chronostasis occurs in the other three conditions would suggest whether debut chronostasis is limited to the visual modality only, intra-modal, or supra-modal in nature. In Experiment 2, the second instead of the first item varied in duration across trials. As expected from Chapter III, debut chronostasis would greatly diminish, if not entirely disappear. Whether the decrement/nullification of debut chronostasis occurs intra-modally, supra-modally, or both would suggest the processing level of the internal duration template.

4.3 Materials and Methods

4.3.1 Participants

All experiment protocols were approved by the institutional review board of California Institute of Technology (Caltech). The observers were drawn from the Caltech brain science subject pool, which mainly consisted of Caltech and Pasadena City of College students. In Experiment 1, there were 19 observers (12 female; 18 naïve; 19-54 years; M = 29.2; SD = 8.2). In Experiment 2, there were 8 observers (4 female; 8 naïve; 18-27 years; M = 20.4; SD = 3.1). All participants provided written informed consent before the experiments. The naïve participants were paid for their cooperation.

4.3.2 Apparatus

The stimuli were presented using a Philips Brilliance 202P7 monitor in Experiment 1 and Lacie Electron 22 Blue IV monitor in Experiment 2. The screen resolution was set at 800 (H) x 600 (V) with frame rate 120Hz. The viewing distance was 70cm. The stimuli presentation code was written in Python with PsychoPy toolbox (Peirce, 2007) under Mac OS X. To ensure that the timing was precise, a preemptive setting was adopted to override other background processes.

4.3.3 Design

A two-way repeated measures factorial design with modality pair (intra-modality or inter-modality) and the modality of the first item (visual or auditory) was implemented, resulting in “V-V”, “A-A”, “V-A”, and “A-V” conditions. The dependent variable was debut chronostasis magnitude (DCM), whose measurement is described in the later subsections. DCMs were analyzed with a two-way analysis of variance (ANOVA) in each experiment.

4.3.4 Stimuli

All stimuli were presented at the center of the screen where there was a constant red fixation point spanning 0.1° (H) x 0.1° (V) visual angle at the center of the screen. The background was black. In both experiments, the visual stimulus was a white disc with radius 1.5° visual angle (Fig 4.1B). The auditory stimulus was a 500 Hz sine wave tone sampled at 44100 Hz. The saliency of the visual and auditory items was matched by the experimenter to be subjectively about equal. Although loudness and luminance affect judged duration of the auditory and visual items, respectively (e.g., Goldstone, Lhamon, & Sechzer, 1978), tuning the relative saliency between the visual and auditory items do not affect the basic phenomenon that auditory items are perceived to last longer than visual ones with the same physical duration (Goldstone & Lhamon, 1974).

4.3.5 Procedure

The dependent variable DCM was derived from the psychometric function estimated by the method of constant stimuli (see the subsection below for details), In Experiment 1, the participants' task was to judge whether the duration of the first item was shorter or longer than the second one in the four-item sequence. The first item was the item that varied in duration across trials but the participants were not specifically made aware of this manipulation. In Experiment 2, the participants' task was to judge whether the duration of the second item was shorter or longer than the first one instead. The second item was the item that varied in duration across trials but the participants were not specifically made aware of this manipulation either. They were forced to make their best guess and to choose either target perceived "longer" or "shorter" using one of two keys on the computer keyboard. The first two items were among the combinations of "V-V", "A-A", "V-A", and "A-V", while the latter two items were each from a random modality per trial.

In each trial, four items were presented one at a time. The participants were also instructed to respond only after all items had been presented. This long gap between the target item presentation and the response helped avoid chronostasis induced by action preparation (e.g., Hagura et al., 2012). Duration of all items except the first was fixed at 600 ms. Centered around that standard duration, the target duration varied in 8 levels from 250 to 950 ms in 100 ms steps. Each inter-stimulus interval (ISI) was random, chosen from a uniform distribution between 250 and 500 ms. Each inter-trial interval (ITI) was random, chosen from a uniform distribution between 1200 and 1600 ms.

Both experiments comprised 1 practice block and 20 experimental blocks. The practice block consisted of 8 trials from the most extreme durations from each condition. During practice, participants were required to verbalize their answer as “first item longer” or “first item shorter” before their button response. Among the experimental blocks, every 5 of them was from the same condition among “V-V”, “A-A”, “V-A”, and “A-V”. The order of block types was randomly shuffled per participant. The experiment typically took about 40 minutes. Each of the experiment blocks contained two randomly shuffled repeats of all 8 durations of the first item. Before every block, an instruction screen indicated the chance to take a short break.

4.3.6 Psychometric Function and Debut Chronostasis Magnitude

In each sequence type and target serial order combination, the probability of a participant reporting the target as subjectively longer than the reference were calculated. A cumulative Gaussian distribution was fitted to those data to estimate psychometric functions. The point of subjective equality (PSE) of each condition was the corresponding physical duration when the probability was 0.5 on the psychometric function. Debut chronostasis magnitude was thus defined as DCM = reference duration - PSE. For example, a 500 ms first item subjectively equivalent to a 600 ms 2nd item this way indicates DCM of 100 ms.

4.4 Results

4.4.1 Experiment 1: Varying The First Item

Crossing the factors modality pair and first item modality resulted in 4 conditions per participant. A two-way 2 (modality pair) x 2 (first item modality) repeated measures ANOVA was performed on the measured DCM. First, as explained in the introduction, it is an open possibility that auditory debut chronostasis may exist in addition to visual debut chronostasis when rhythmic cues are unreliable (i.e. with random ISI). (1) If it turned out that intramodally, the DCM of visual and auditory cases were similar, it would suggest that similar operation principles underlie visual and auditory duration estimation, or that duration estimation operates supramodally. (2) If DCM were similar in the intra- (average of V-V and A-A conditions) and inter-modal (average of V-A and A-V conditions) cases, it would imply that debut chronostasis were basically a supramodal phenomenon. (3) If DCM were weaker in the inter-modal than in the intra-modal cases, it would imply that both within- and cross-modal duration estimation mechanisms exist. (4) If DCM were zero in the inter-modal cases, it may suggest that sensory cortices are the foundations of duration estimation. As will be explained in the next paragraph, the results are consistent with (1) and (3) above.

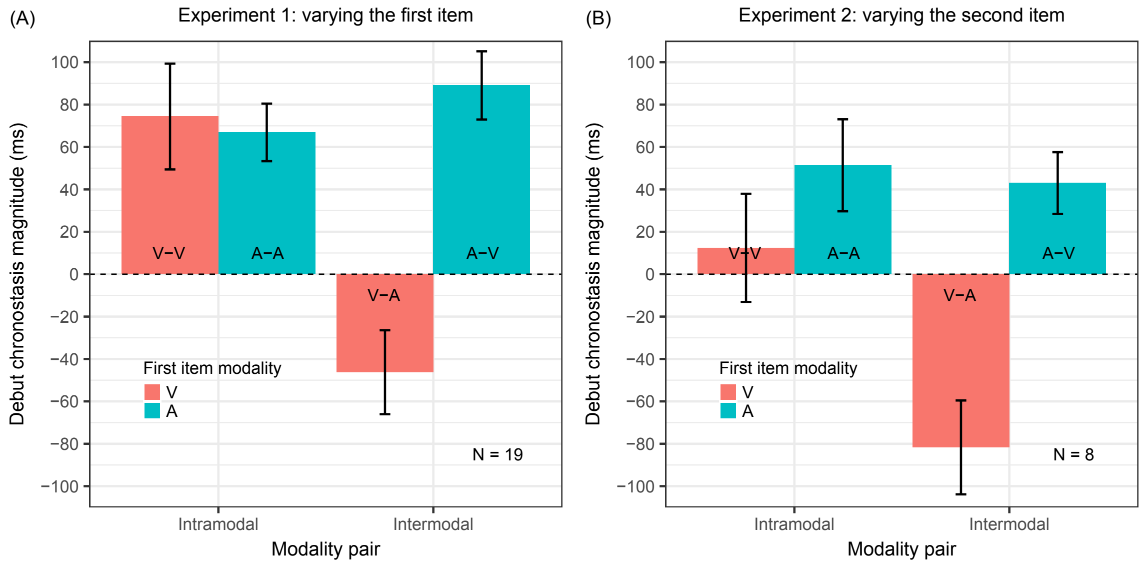

Fig 4.1. Results in Experiments 1 and 2.

Vertical axis is debut chronostasis magnitude (DCM, the amount of subjective time expansion of the first item relative to the second one, see methods and supplementary methods for details). (A) Experiment 1 evidently demonstrates the existence of auditory debut chronostasis with similar strength as visual debut chronostasis. Consistent with the literature, the intermodal results show that auditory items were overestimated compared to visual items. (B) When varying the second item instead in Experiment 2, as explained in Chapter III, DCM is largely reduced due to reduction of internal duration template uncertainty that mostly relies on the first item. This reduction in DCM appears to be constant across all four conditions. See Fig 4.2 for further analysis across Experiments 1 and 2.

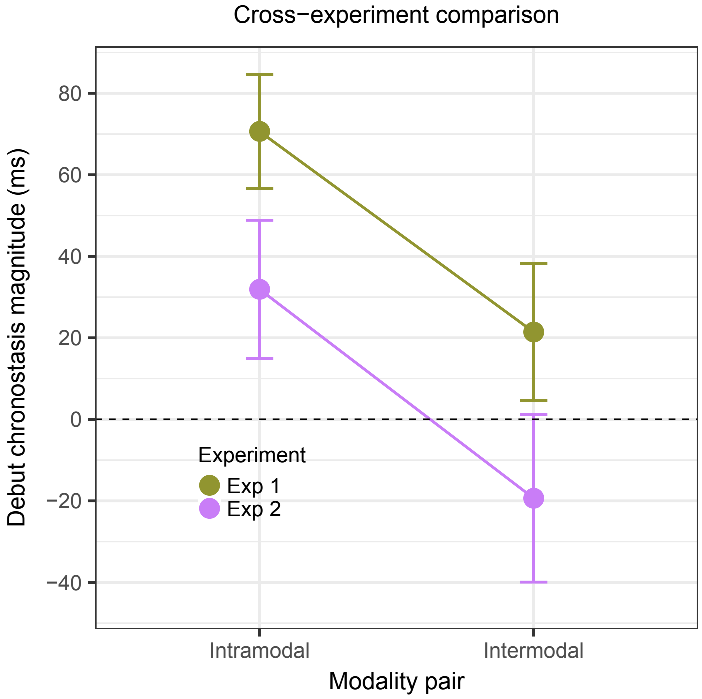

Fig 4.2. Cross-experiment comparison.

This figure shows the intra- (average of V-V and A-A conditions) and inter-modal (average of V-A and A-V conditions) DCM in Experiments 1 (yellow dots) and 2 (purple dots). In both experiments, DCM is higher in the intramodal than in the intermodal condition. From Experiment 1 to 2, the variable item across trials changed from the first item to the second item. As demonstrated in Chapter III, debut chronostasis should be reduced because the internal duration template is more certain in Experiment 2. Apparently, the parallel shift from the yellow line to the purple line suggests that the DCM reduction effect is supra-modal. The result that DCM is higher in the intramodal than in the intermodal condition and the result of supramodal DCM reduction seem to be two linearly additive effects. See text for interpretations.

Fig 4.1A summarizes the results (N = 19) from Experiment 1. The main effect of modality pair was significant ($F_{1,18} = 12.03$, $P < 0.01$, $\eta_p^2 = 0.40$). The main effect of first item modality was significant ($F_{1,18} = 25.00$, $P <$ 1e-4, $\eta_p^2 = 0.58$). The interaction effect of modality pair and first item modality was also significant ($F_{1,18} = 20.12$, $P <$ 1e-3, $\eta_p^2 = 0.53$). Furthers simple main effect analysis given each modality pair revealed significant effect between V-A and A-V conditions ($F_{1,18} = 44.69$, $P <$ 1e-5, $\eta_p^2 = 0.71$) but not between the V-V and A-A conditions ($F_{1,18} = 0.13$, $P = 0.72$, $\eta_p^2 = 0.01$). Simple main analysis given each first item modality dimension revealed significant effect between V-V and V-A conditions ($F_{1,18} = 17.77$, $P <$ 1e-3, $\eta_p^2 = 0.50$), but not between A-A and A-V conditions ($F_{1,18} = 5.43$, $P = 0.03$, $\eta_p^2 = 0.23$, Bonferroni multiple comparison correction applied to alpha level). Therefore, the source of interaction was the significant difference between V-A and A-V, as well as between V-V and V-A conditions.

Contrary to the findings of Rose and Summers (1995), the novel discovery here was that debut chronostasis also exists in the auditory domain, not just in the visual domain. DCM was similar between the visual and auditory senses. The major difference between our study and Rose and Summers' is that they used sequences with fixed ISI. When the standard duration and the ISI are both fixed, one can anticipate the onset and offset timings in an auditory sequence. For instance, in an oddball chronostasis paradigm with fixed ISI, early and late oddballs were perceived as shorter and longer, respectively. On-time oddballs were least distorted in subjective duration (McAuley & Fromboluti, 2014). In other words, in the auditory domain, rhythm perception can potentially correct illusions in duration perception. Anecdotally, from our pilot results, it is harder to do so within a visual sequence.

In Fig 4.1A, the intermodal results were consistent with the literature in several aspects. First, it is well-established that auditory durations are perceived subjectively longer than visual ones (e.g., Goldstone & Lhamon, 1974; Ulrich, Nitschke, & Rammsayer, 2006; Wearden, Edwards, Fakhri, & Percival, 1998). Second, as Goldstone and Lhamon (1974) described, intramodal duration ratings were 'sandwiched' between intermodal duration ratings. In our results, the DCM also exhibited a similar pattern. This led us to further ask, apart from the apparent longer duration in sounds than in flashes, is the average DCM comparable between the intra- and inter-modal conditions?

In the results of Experiment 1, debut chronostasis appeared to only exist in the intra-modal conditions. Post-hoc two-tailed t-tests showed that the average intra-modal DCM (70.6 ms) was significantly greater than 0 ($t_{18} = 4.09$, $P < 1e\text{-}3$) while the average inter-modal DCM (21.4 ms) was not ($t_{18} = 1.43$, $P = 0.17$). However, either empirically (e.g., Goldstone & Lhamon, 1974; Ulrich, Nitschke, & Rammsayer, 2006; Wearden, Edwards, Fakhri, & Percival, 1998) or theoretically (Ulrich, Nitschke, & Rammsayer, 2006), the absolute DCM in the V-A and A-V conditions could be asymmetric in most cases. Therefore, in Experiment 2, we measured the asymmetry in absolute DCM between the V-A and A-V conditions when debut chronostasis was largely reduced when the second item varied in duration across trials instead of the first item (Chapter III). With this baseline information, we could infer whether debut chronostasis is within- or supra-modal in nature. The results of Experiment 2 turned out to support both within- and supra-modal factors underlying debut chronostasis.

4.4.2 Experiment 2: Varying The Second Item

The variable item became the second one in Experiment 2. Everything else was the same. The definition of DCM was also modified to be comparable with that in Experiment 1. Crossing the factors modality pair and first item modality resulted in 4 conditions per participant. A two-way 2 (modality) x 2 (first item modality) repeated measures ANOVA was performed on the measured DCM. As in Chapter III, we predict that auditory debut chronostasis would become largely, if not completely, reduced when the first item does not vary in duration across trials. This is because a fixed duration first item could naturally serve as a new internal duration template with virtually the same value as an existing one. If the average inter-modal DCM between the V-A and A-V conditions stayed the same in Experiment 2, it would indicate that debut chronostasis is an intramodal phenomenon and the duration memory template might be stored in each modality. On the contrary, if the average inter-modal DCM diminished with the magnitude as the average intra-modal DCM in Experiment 2 compared to Experiment 1, it would imply that debut chronostasis has a supra-modal component and the duration memory template might be stored in a supra-modal region. Other intermediate results would suggest the existence of both within- and cross-modal mechanisms in duration perception memory.

Fig 4.1B summarizes the results (N = 8) from Experiment 2. Despite of the relatively low number of participants, the main effect of modality pair was significant ($F_{1,7} = 5.97$, $P < 0.05$, $\eta_p^2 = 0.46$); the main effect of first item modality was significant ($F_{1,7} = 30.26$, $P <$ 1e-3, $\eta_p^2 = 0.81$); the interaction effect of modality pair and first item modality was also significant ($F_{1,7} = 5.76$, $P < 0.05$, $\eta_p^2 = 0.45$). Further simple main analysis within each modality pair revealed significant effect between V-A and A-V conditions ($F_{1,7} = 18.23$, $P < 0.01$, $\eta_p^2 = 0.72$) but not between V-V and A-A conditions ($F_{1,7} = 6.65$, $P = 0.04$, $\eta_p^2 = 0.49$, Bonferroni multiple comparison correction applied to alpha level). Simple main analysis within each first item modality revealed significant effect between V-V and V-A ($F_{1,7} = 12.89$, $P < 0.01$, $\eta_p^2 = 0.65$), but not between A-V and A-A conditions ($F_{1,7} = 0.08$, $P = 0.78$, $\eta_p^2 = 0.01$). Therefore, same as with the results in Experiment 1, the source of interaction was the significant difference between V-A and A-V, as well as that between V-V and V-A conditions.

Post-hoc two-tailed t-tests showed that the average intra-modal DCM (31.9 ms) was not significantly different from 0 ($t_7 = 1.42$, $P = 0.20$) and the average inter-modal DCM (-19.4 ms) was not either ($t_{18} = -1.65$, $P = 0.14$). Due to the time limitation, the limited number of participants (N=8) may not reach sufficient power to reject these null hypotheses.

4.4.3 Cross-Experiment Comparison

In order to examine whether debut chronostasis is an intra-, a supra-modal phenomenon, or both, the average DCM in the intra- (V-V and A-A) and inter-modal (V-A and A-V) conditions in both Experiments 1 and 2 was replotted in Fig 4.2. The pattern clearly showed that the results in Experiment 2 was a parallelly downward shifted version of those in Experiment 1. Between Experiments 1 and 2, the DCM differences were 38.7 ms in the intra- and 40.8 ms in the inter-modal conditions. As explained in Chapter III, the decrement of DCM from Experiment 1 (yellow points) to Experiment 2 (purple points) was because the internal duration template is more certain in Experiment 2. The parallel shift suggests that the DCM decrement effect is supra-modal. Additionally, in both experiments, DCM was higher in the intramodal than in the intermodal condition. The exact reason for this is not yet clear, but it at least suggests an intra-modal stage of duration perception. With the parallel shift pattern, the intra-modal effect that DCM is higher in the intramodal than in the intermodal condition and the supra-modal effect of DCM reduction appears to linearly additive. Overall, the results reveal that the original visual debut chronostasis (Cai, Eagleman, & Ma, 2015; Pariyadath & Eagleman, 2007; Rose & Summers, 1995; see also Chapter III) mixed intra-modal and supra-modal effects.

4.5 General Discussion

4.5.1 Main Findings and Interpretations

There were three novel discoveries in this study. First, debut chronostasis also exists in the auditory domain, as shown in Experiment 1 (Fig 4.1A). The reason why Rose and Summers (1995) found only visual but not auditory debut chronostasis could be that they used fixed ISIs. The auditory modality is known to possess better temporal acuity than the visual modality (e.g. Rammsayer, Borter, and Troche, 2015). Fixed ISIs also inevitably lead to the build-up of rhythmic anticipation of item onsets and offsets (e.g., McAuley & Fromboluti, 2014). Therefore, fixed ISIs in Rose and Summers (1995) could make auditory duration distortions harder to occur. Second, across Experiments 1 and 2, average DCM was higher in intra- and lower in inter-modality conditions (Fig 4.2). This suggests that duration perception has an intra-modal stage. Third, debut chronostasis can be modulated by a similar amount after exchanging the presentation order of the variable and the constant items in all modality conditions: V-V, A-A, V-A, and A-V, as shown by the differential results between Experiments 1 and 2 (Fig 4.1A and B). This suggests that a supra-modal stage of duration discrimination exists on top of the intra-modal mechanisms. The information integration of these two stages seem to be linearly additive, as evidenced by the parallel lines in Fig 4.2. Therefore, overall the results suggest that debut chronostasis involve both intra- and supra-modal mechanisms.

Our results thus suggest a novel possibility that there could be both intra- and supra-modal stages of duration memory storage. As presented in Chapter III, the working theory of visual debut chronostasis is the internal duration uncertainty hypothesis. Only when the first item in a multi-item sequence varies in duration across trials does it induce large uncertainty to the average internal duration template maintained over trials, which eventually leads to debut chronostasis, possibly through elevated implicit attention or memory encoding demands. Therefore, both modality-dependent and modality-independent duration standards may exist.

4.5.2 Implications to Existing Theories

If both intra- and supra-modal stages of duration memory storage were at play, the implications of our findings would bring interesting developments to existing theories. For example, a popular version of time-perception information-processing models, the scalar expectancy theory, or *SET* (Gibbon, Church, & Meck, 1984), postulates an internal pacemaker emitting pulses gated by a switch before reaching working memory. For discrimination tasks, the memory traces in the reference memory and the working memory are compared. To explain how sounds appear to last longer than lights, several studies (Penney, Gibbon, & Meck, 2000; Ulrich, Nitschke, & Rammsayer, 2006; Wearden, Edwards, Fakhri, & Percival, 1998) have applied this theory on their psychophysical data and attributed the difference between visual and auditory signals to the difference in pacemaker speed. Although not stated explicitly, these studies implicit assume that separate pacemakers exist in different modalities. In comparison, in light of the internal duration uncertainty hypothesis as advanced in Chapter III, our findings here suggest that even the memory stage may contain both intra- and supra-modal components in duration judgment.

Nevertheless, there is still a big gap between the earlier well-developed quantitative psychophysical models, such as SET, and recent neural imaging findings on contrasting intra- and inter-modality duration perception. With functional magnetic resonance imaging (fMRI), Harrington, Castillo, Fong, and Reed (2011) adopted a two-item, standard-followed-by-test duration discrimination task and found neural correlates in multiple distributed brain regions. The phenomenon of auditory signals appearing to last longer than visual ones correlated with activation of higher sensory areas, superior temporal, posterior insula, and middle occipital area, accompanied by stronger effective connectivity in the V-A condition only. The contrast between intra- and inter-sensory conditions correlated with decreased striatal and increased superior parietal activity. These areas showed higher connectivity strength with vision, memory, and cognitive control regions during intersensory timing. Nevertheless, since they did not specifically find debut chronostasis, future studies could utilize our main finding that the intra-modal and supra-modal components of debut chronostasis are linearly additive to tease apart debut chronostasis from the visual-auditory duration difference.

To bridge the gap, our contributions here is the dissociation of debut chronostasis from the modality-dependent difference of duration perception (i.e. apparent longer duration in sounds than in lights), as well as the demonstration of their linear additivity. Based on SET, while the apparent longer duration of auditory than visual stimuli has been attributed to modality-specific pacemaker rate difference, our results can help future studies refine the neural correlates of modality-dependent and modality-independent memory components.

4.5.3 Two-items vs. Four-items

Debut chronostasis has been repeated shown in several studies with multi-item (four or five) paradigms (Cai, Eagleman, & Ma, 2015; Pariyadath & Eagleman, 2007; Rose &

Summers, 1995), as well as Chapter III and this chapter, but it is not as evident in two-item paradigms (e.g. Goldstone & Lhamon, 1984; Ulrich, Nitschke, & Rammsayer, 2006). The internal duration memory template hypothesis (Chapter III) can explain this because it is easier to maintain and rely on such an internal template for comparative judgments whenever standards (fixed duration) appear more frequently than the test item (variable duration). For instance, in experiment 1 of Ulrich et al. (2006), where the variable item was the second one of the two-item sequence, their DCM pattern is strikingly similar to that in our Experiment 2. In their results, averaging across the 100 and 1000 ms standard conditions, DCM was 6, 18, -68, and 32 ms, respectively, in the V-V, A-A, V-A, and A-V conditions (compare against our Fig 4.1B). In other words, debut chronostasis was close to 0 in their intra-modal conditions. In their experiment 3, when the first item varied in duration instead (as in our Experiment 1), averaging across the 100 and 1000 ms standard conditions, DCM was about -15, -10, -100, and 40 ms (by eyeball estimation), respectively, in the V-V, A-A, V-A, and A-V conditions (compare against our Fig 4.1A). Even though their V-A and A-V DCM pattern was similar to our Experiment 2, their intra-modal V-V and A-A DCM was still close to 0. It is not entirely clear whether this is because they used only two items or because they used fixed ISI. Therefore, the exact necessary conditions of debut chronostasis warrants future research.

4.5.4 Alternative Interpretations

In the results of Experiment 1, the lack of debut chronostasis in the inter-modal conditions may also be explained by the repetition suppression hypothesis. Since the repetition suppression hypothesis assumes that sensory cortex neural response magnitude directly encodes subjective duration (Eagleman & Pariyadath, 2009), repetition suppression supposedly does not occur in the intermodal conditions. In this sense, the supramodal debut chronostasis reduction from Experiment 1 to Experiment 2 can still be explained by the internal duration uncertainty hypothesis (Chapter III), while the higher average DCM in the intramodal than in the intermodal conditions can be explained by repetition suppression. If this were true, with reasonably sufficient number of samples in Experiment 2, the average DCM in the intra-modal condition may turn out to be significant.

4.5.5 Limitations

It remains to be seen whether each aspect of debut chronostasis effect is additive or multiplicative. If it is additive, it should be independent of standard duration; if it is multiplicative, it should be proportional to standard duration. In the SET, additive effects are associated with the switch onset and offset timing shift; multiplicative effects imply pacemaker or accumulator (memory) processes. If our hypothesis that internal duration memory uncertainty elicits debut chronostasis were correct (Chapter III), it would predict multiplicative instead of additive effects. Since we did not manipulate the standard durations, future studies may explore this specific prediction.

4.6 Conclusions

This is the first study that demonstrates the existence of auditory debut chronostasis effect, which has comparable magnitude to visual debut chronostasis (Experiment 1). We also provided a potential explanation of the discrepancy with regard to the null result in the literature, i.e. variable vs. fixed ISIs. In inter-modal conditions, on top of the known phenomenon that sounds are judged as lasting longer than lights, the average of the two inter-modal conditions (V-A and A-V) did not reveal debut chronostasis. In Experiment 2, when the second instead of the first became the variable item, as expected from the main finding in Chapter III, the reduction in debut chronostasis magnitude seemed to be equal in all conditions (V-V, A-A, V-A, and A-V). In other words, debut chronostasis is stronger in intra-modal conditions, but its modulation due to duration memory trace certainty is supra-modal. Therefore, debut chronostasis involves both intra- and supra-modal stages.

4.7 Acknowledgements

This work was supported by the National Science Foundation (NSF BCS-1439372) and Japan Science and Technology Agency CREST to Shinsuke Shimojo (principal investigator).

The authors declare that there are no commercial relationships.

Chapter V

TRACING NEURAL SIGNATURE OF CHRONOSTASIS BY VISUAL FLICKER

5.1 Abstract

As a follow-up study of Chapter II, we were motivated to examining whether perceived duration might be encoded as sensory cortex neural response amplitude using EEG. This idea has been an assumption underlying the repetition suppression theory of oddball chronostasis (see Chapter II). To examine the neural correlates of time perception, we chose electroencephalography (EEG) as the neural imaging tool that has high temporal resolution. We were also interested in applying a fruitful method that has been widely applied in vision EEG studies, the "steady-state visual evoked potential (SSVEP)", to subsecond time perception, to fully utilize the temporal resolution of EEG and to study time perception mechanisms in the time-frequency domain. In Experiment 1, we first established that oscillating the luminance of the visual stimuli in the oddball paradigm did not change the direction and amount of oddball chronostasis. In Experiments 2 and 3, we tested specific EEG predictions that follow the attention enhancement and the repetition suppression theories as introduced in Chapter II. The data support the former but oppose the latter theory. Our contribution was to apply the SSVEP method to study factors of subsecond time perception for the first time. The results further corroborate our psychophysical findings in Chapter II.

5.2 Introduction

How exactly the human brain stores subsecond duration information remains largely unclear. Some researchers suggest that narrowly-tuned, overlapping duration channels mediate human time perception (Heron et al., 2011). However, with a duration adaptation paradigm, Curran et al. (2016) found that the channel-based model is not a sufficient explanation. On the other hand, Eagleman and Pariyadath (2009) proposed that subjective duration may be stored in terms of sensory cortical neural response amplitude.

Although the first stage of duration information storage may not be easy to pin down directly, our strategy is to utilize duration illusions to understand how duration perception is modulated, as hints to possible formats of duration information storage. In this study, we contrasted the attention enhancement (New & Scholl, 2009; Tse et al., 2004) and the repetition suppression theories (Cai, Eagleman, & Ma, 2015; Pariyadath & Eagleman, 2007, 2012; Schindel, Rowlands, & Arnold, 2011) of oddball chronostasis (see Chapter II) using EEG.

Based on prior literature, EEG provides specific predictions regarding the attention enhancement and repetition suppression theories. For attention enhancement, many studies have reported alpha band (8-12 Hz) power correlates with attention in the parietooccipital cortex. For example, when the target and distractor stimuli are presented in opposite visual hemifields, the alpha band power contralateral to the target decreases while that contralateral to the distractor increases (Kelly, Lalor, Reilly, & Foxe, 2006). This reduction of alpha band power contralateral to the attended visual hemifield can start as early as 200 ms before target onset (Sauseng et al., 2005), indicating anticipatory effects of attention. Given rhythmic trial structure, alpha band power could also decrease regularly (Rohenkohl & Nobre, 2011). Behaviorally, individual differences in alpha band power modulation also predicted reaction times (Gould, Rushworth, & Nobre, 2011). Therefore, if attention prolongs perceived time, there should be alpha band power decrement associated with it.

As for the repetition suppression theory, it has been shown that response defined as a "steady-state visual evoked potential (SSVEP)" (Regan, 1966) reduces as the stimuli repeat (e.g., Martens & Gruber, 2012; Nemrodov, Jacques, & Rossion, 2015). SSVEPs are EEG response measures when the property of some stimulus is modulated periodically, which are also dubbed "frequency tagging" (for a review, see Norcia, 2015). Typically, the stimulus modulation is luminance flicker around 10 Hz, but periodic modulation of other properties such as orientation or hue also generate SSVEPs. The principle is that when an external stimulus oscillates periodically, part of the internal neural responses also oscillates at the same frequency, resulting to high signal-to-noise-ratio, compared to traditional time-domain event-related potentials (ERPs). Also, when the inter-stimulus interval is at the subsecond range, the ERPs of separate stimuli tend to overlap in time; on the other hand, SSVEPs provide a neural activity measure localized in both time and frequency. Therefore, here we utilize the strengths of SSVEP to test if the repetition suppression theory correctly predicts the neural activity pattern. The prediction would be that as the same visual items are being presented, the corresponding SSVEP decreases with repetition and recovers whenever an occasional distinct item appears (Eagleman & Pariyadath, 2009).

In Experiment 1, we first established that frequency tagging does not change the phenomenon of oddball chronostasis, given that the tagging frequency is the same for the standards and the target in the oddball paradigm (see Chapter II). In Experiment 2, we studied frequency tagging using 15 Hz stimuli. In Experiment 3, we used 20 Hz frequency tagging to confirm that the results were not tagging frequency specific.

5.3 Materials and Methods

5.3.1 Participants

All experiment protocols were approved by the institutional review board of California Institute of Technology (Caltech). The observers were drawn from the Caltech brain science subject pool, which mainly consisted of Caltech and Pasadena City of College students. In Experiment 1, there were 14 observers. In Experiment 2, there were 13 observers (6 female; 12 naïve; 18-38 years; M = 23.9; SD = 7.2). In Experiment 3, there were 11 observers (5 female; 10 naïve; 18-42 years; M = 24.5; SD = 6.9). All participants provided written informed consent before the experiments. The naïve participants were paid for their cooperation.

5.3.2 Apparatus

The stimuli were presented using an Iiyama Vision Master Pro 513 monitor in all three experiments. The screen resolution was set at 800 (H) x 600 (V) with frame rate 120Hz. The viewing distance was 70cm. The stimuli presentation code was written in MATLAB with Psychtoolbox (Brainard, 1997; Pelli, 1997) under Mac OS X. To ensure that the timing was precise, a preemptive setting was adopted to override other background processes.

5.3.3 Design

In Experiment 1, a trial consisted of 3-5 standards (500 ms white squares) followed by an oddball (white disc lasting 250-600 ms in 50 ms steps) and a standard, with a fixed inter-stimulus interval of 310 ms. Each trial consisted of stimuli that were either all static or flickering at 20 Hz. Observers judged whether the oddball was longer or shorter than the standard. In Experiments 2 and 3, participants performed the above task with 15 Hz and 20 Hz flickering stimuli, respectively, while their EEG was recorded. Each condition was repeated 15 times resulting in 360 trials.

5.3.4 Stimuli

All stimuli were presented at the center of a black screen where there was a constant red (CIE x = 0.614, y = 0.342, Y = 26.1) fixation point spanning 0.1° (H) x 0.1° (V) visual angle at the viewing distance of 70 cm. In Experiment 1, the white discs had 5.7° diameter and the white squares had 5.1° width, resulting to equal area on the screen. In Experiment 2, the standard stimuli were 5.1° x 5.1° squares that flickers between white and black in 15 Hz; the deviant was a 15 Hz flickering circle. As validated in Experiment 1, when the standards and the deviant had the same flickering frequency, the oddball chronostasis magntitude was comparable to that induced by static stimuli. In Experiment 3, the parameters were as in Experiment 2 except that the flickering frequency was 20 Hz.

5.3.5 Procedure

The procedure for determining the psychometric function was the same as in Chapter II. The psychometric function was obtained to derive the Point of Subjective Equality (PSE=duration at 50% probability of responding ‘longer’). The Subjective Time Expansion Factor (STEF) was defined as standard duration / PSE.

5.3.6 EEG Acquisition and Analyses

EEG was recorded by an EGI amplifier system with the HydroCel 128 channel Geodesic Sensor Net with Cz as the reference channel. The sampling frequency was 1000 Hz. During the visual stimuli presentation, a digital output device registered visual event timings by sending TTL signals to the amplifier. Data analysis and visualization were performed using the Brainstorm (Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011) and the FieldTrip (Oostenveld, Fries, Maris, & Schoffelen) toolboxes in MATLAB. Electrode names followed the international 10-20 system. The raw EEG waveforms went through a notch filter for electricity line noise at 60 Hz and harmonics, signal-space projection for eye blinking component removal using signals from channels Fp1 and Fp2, and then down sampling to 100 Hz. Epoch were defined as the time period between 750 ms before the first item onset and 500 ms after the last item offset, where the pre-first item period served as the baseline for DC offset correction. ERPs were calculated by averaging the epochs in the same condition. Time-frequency representations (TFRs) of the epochs were performed using Morlet wavelets. The total magnitude of TFRs were decomposed into evoked (phase-locked) and induced (non-phase-locked) components following the convention by Bertrand & Tallon-Baudry (2000). The total TFR magnitude per condition was the average of single trial TFRs; the evoked TFR magnitude per condition was the TFR of averaged epochs; the induced TFR magnitude per trial was the difference between total and evoked TFR magnitude. All TFRs were baselined by the 500 ms period before the first item onset. The TFR magnitudes were group averaged and tested statistically. To correct for type I error in multiple comparison, false discovery rate (Benjamini & Hochberg, 1995) was controlled at the level of 0.05 in parametric Student’s t-tests across electrodes.

5.4 Results

5.4.1 Experiment 1: Behavior

In the visual oddball task, both static and flickering stimuli produced significant subjective time expansion effects ($p < .001$ for both). The STEF ranged from 0.91 to 1.37 for static stimuli and from 1.03 to 1.29 for flickering stimuli across all subjects. Kolmogorov–Smirnov tests showed no significant difference between the psychometric functions of static and flickering stimuli ($p > .5$ for all subjects). Hence, the subjective time expansion effect holds for flickering stimuli. Fig 5.1 shows the similarity in psychometric functions across the static and flickering conditions.

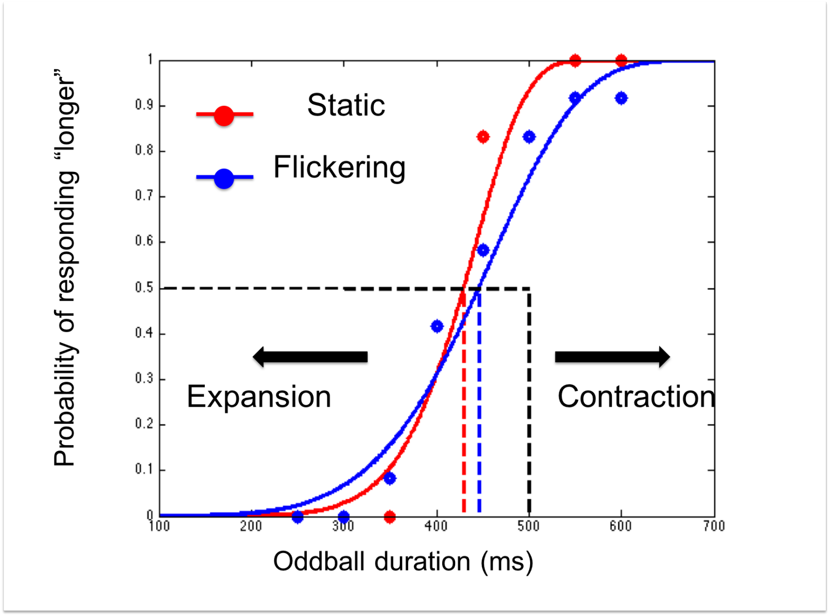

Fig 5.1. Comparing psychometric functions of static and flickering items in the oddball paradigm (Experiment 1).

Given the 500 ms standards, the amount of departure of the PSE from the standard duration indicates the illusion strength. Note that the psychometric functions are similar between the static and 20 Hz flickering conditions.

5.4.2 Experiment 2: 15 Hz Frequency Tagging

Similar to previous repetition suppression studies (e.g., Martens & Gruber, 2012; Nemrodov, Jacques, & Rossion, 2015), the TFR magnitude dynamics at the tagged band (15 Hz) provides a test for the repetition suppression hypothesis. Fig 5.2A shows the group-averaged (N = 11) topographic plot of the electrodes that respond to the stimulus flickering frequency. Oz was the electrode with maximal magnitude modulation. Therefore, 15 Hz power dynamics at Oz could be the best site for examining the repetition suppression theory. The left column of Fig 5.3A shows the dynamics of group-averaged total TFR magnitude at 15 Hz. The pattern does not support the repetition suppression theory for two clear reasons. First, the first standard and the oddball (the fourth stimulus) do not have the largest magnitude among all items. Second, from the first to the standard before the oddball, there is not a trend of suppression through repetition.

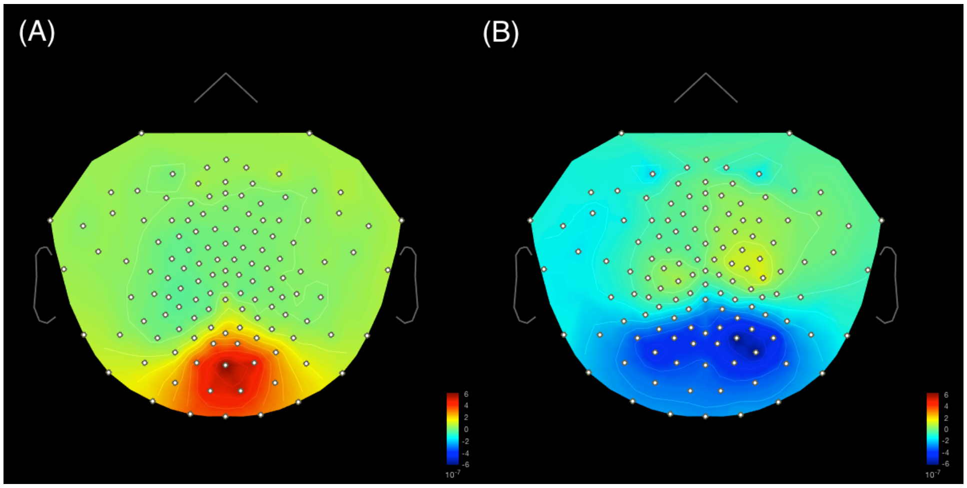

Fig 5.2. TFR magnitude topography at the tagged band (15 Hz) and the alpha band (10 Hz) in Experiment 2.

The electrode with maximal modulation over time is Oz at the tagged band (A) and PO8 at the alpha band (B). The tagged band shows a positive peak at Oz while the alpha band shows two negative peaks centered around PO7 and PO8, respectively.

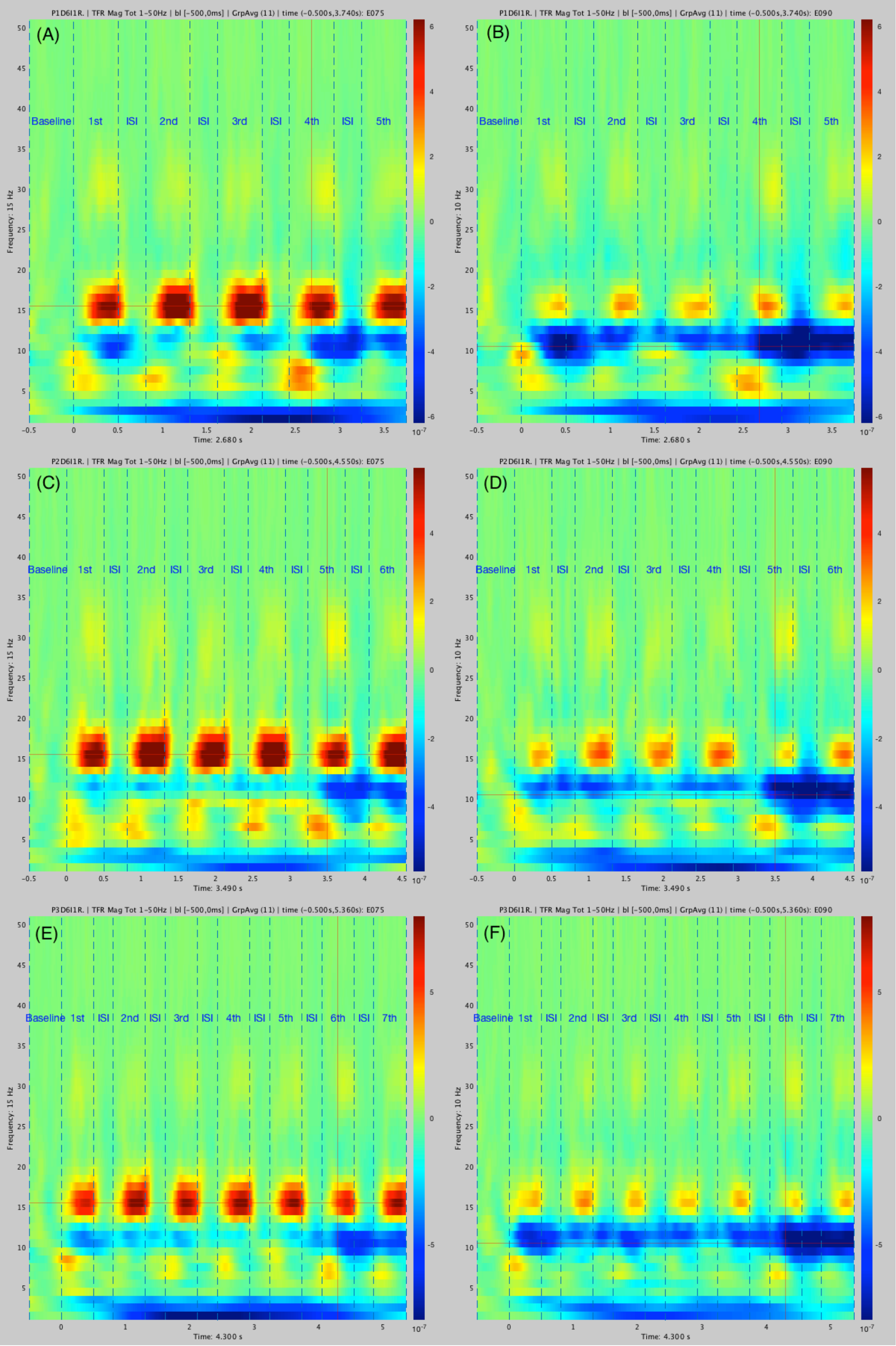
P1D6I1R. | TFR Mag Tot 1-50Hz | bl [-500,0ms] | GrpAvg (11) | time (-0.500s,3.740s): E075
(A)
Baseline 1st ISI 2nd ISI 3rd ISI 4th ISI 5th
Frequency: 15 Hz
Time: 2.680 s
10^-7
P1D6I1R. | TFR Mag Tot 1-50Hz | bl [-500,0ms] | GrpAvg (11) | time (-0.500s,3.740s): E090
(B)
Baseline 1st ISI 2nd ISI 3rd ISI 4th ISI 5th
Frequency: 10 Hz
Time: 2.680 s
10^-7
P2D6I1R. | TFR Mag Tot 1-50Hz | bl [-500,0ms] | GrpAvg (11) | time (-0.500s,4.550s): E075
(C)
Baseline 1st ISI 2nd ISI 3rd ISI 4th ISI 5th ISI 6th
Frequency: 15 Hz
Time: 3.490 s
10^-7
P2D6I1R. | TFR Mag Tot 1-50Hz | bl [-500,0ms] | GrpAvg (11) | time (-0.500s,4.550s): E090
(D)
Baseline 1st ISI 2nd ISI 3rd ISI 4th ISI 5th ISI 6th
Frequency: 10 Hz
Time: 3.490 s
10^-7
P3D6I1R. | TFR Mag Tot 1-50Hz | bl [-500,0ms] | GrpAvg (11) | time (-0.500s,5.360s): E075
(E)
Baseline 1st ISI 2nd ISI 3rd ISI 4th ISI 5th ISI 6th ISI 7th
Frequency: 15 Hz
Time: 4.300 s
10^-7
P3D6I1R. | TFR Mag Tot 1-50Hz | bl [-500,0ms] | GrpAvg (11) | time (-0.500s,5.360s): E090
(F)
Baseline 1st ISI 2nd ISI 3rd ISI 4th ISI 5th ISI 6th ISI 7th
Frequency: 10 Hz
Time: 4.300 s
10^-7

Fig 5.3. Single electrode TFR magnitude plots of Experiment 2.

The left column (A, C, E) shows the group-averaged time-frequency magnitude at electrode Oz. The right column (B, D, F) shows the group-averaged time-frequency magnitude at electrode PO8. The top row (A, B) displays the results in the 5 item condition, where the 4th item is the oddball. The middle row (C, D) displays the results in the 6 item condition, where the 5th item is the oddball. The bottom row (E, F) displays the results in the 7 item condition, where the 6th item is the oddball. At both electrodes, each visual item leaves an unambiguous trace in the time-frequency plot. The tagged band does not follow the predictions of the repetition suppression hypothesis. Consistent with the attention enhancement hypothesis, the alpha band decreases in magnitude at the oddball (see text).

On the other hand, the TFR magnitude dynamics at the alpha band (8-12 Hz, centered around 10 Hz) provides a test for the attention enhancement hypothesis. Fig 5.2B shows the group-averaged topographic plot of the electrodes at 10 Hz. PO8 was the electrode with maximal magnitude modulation. In the literature, it has been shown that the alpha band magnitude decrement associates with attention or temporal expectation (Gould, Rushworth, & Nobre, 2011; Kelly et al., 2006; Rohenkohl & Nobre, 2011; Sauseng et al., 2005). Consistent with this hypothesis, the right column of Fig 5.3 shows that alpha band magnitude has the most magnitude reduction at the oddball. The negative peak of 10 Hz magnitude is later than the positive peak of 15 Hz magnitude.

5.4.3 Experiment 3: 20 Hz Frequency Tagging

To confirm that the results were not specific to 15 Hz frequency tagging, in Experiment 3, the tagging frequency was 20 Hz instead. The pattern was similar to that obtained in Experiment 2. At 20 Hz tagging frequency of the visual items, the TFR magnitude topography in Fig 5.4 resembled that in Figs 5.2. Although the maximal negative modulation in the alpha band was in electrode PO4 instead of PO8, for the sake of comparison, the frequency tagging results in Fig 5.5 were plotted for PO8. The data pattern in Fig 5.5 was consistent with that in Fig 5.3. Therefore, the results were not in Experiment 2 were not specific to the tagging frequency used. This again supported the attention enhancement but not the repetition suppression theory.

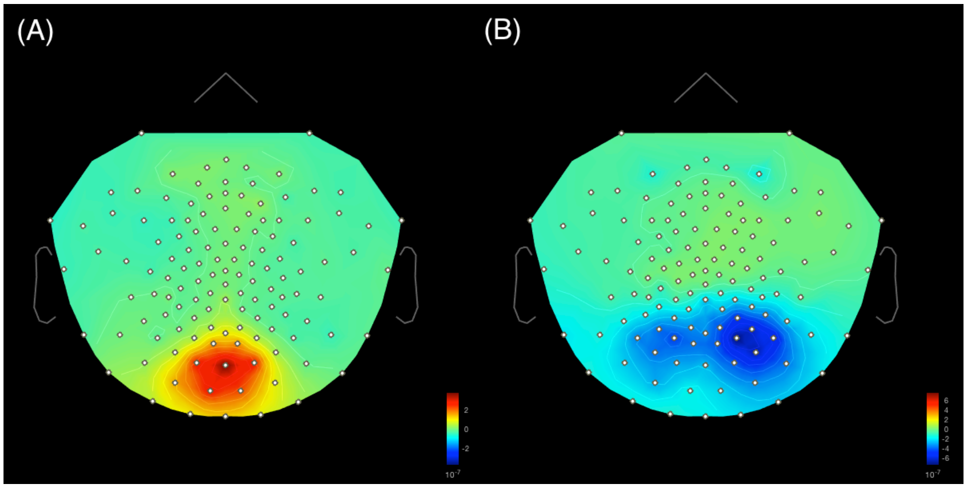

Fig 5.4. TFR magnitude topography at the tagged band (20 Hz) and the alpha band (10 Hz) in Experiment 3.

Similar to Fig 5.2, the electrode with maximal modulation over time is Oz at the tagged band (A) and near PO4 at the alpha band (B). The tagged band shows a positive peak at Oz while the alpha band shows two negative peaks centered around PO3 and PO4, respectively.

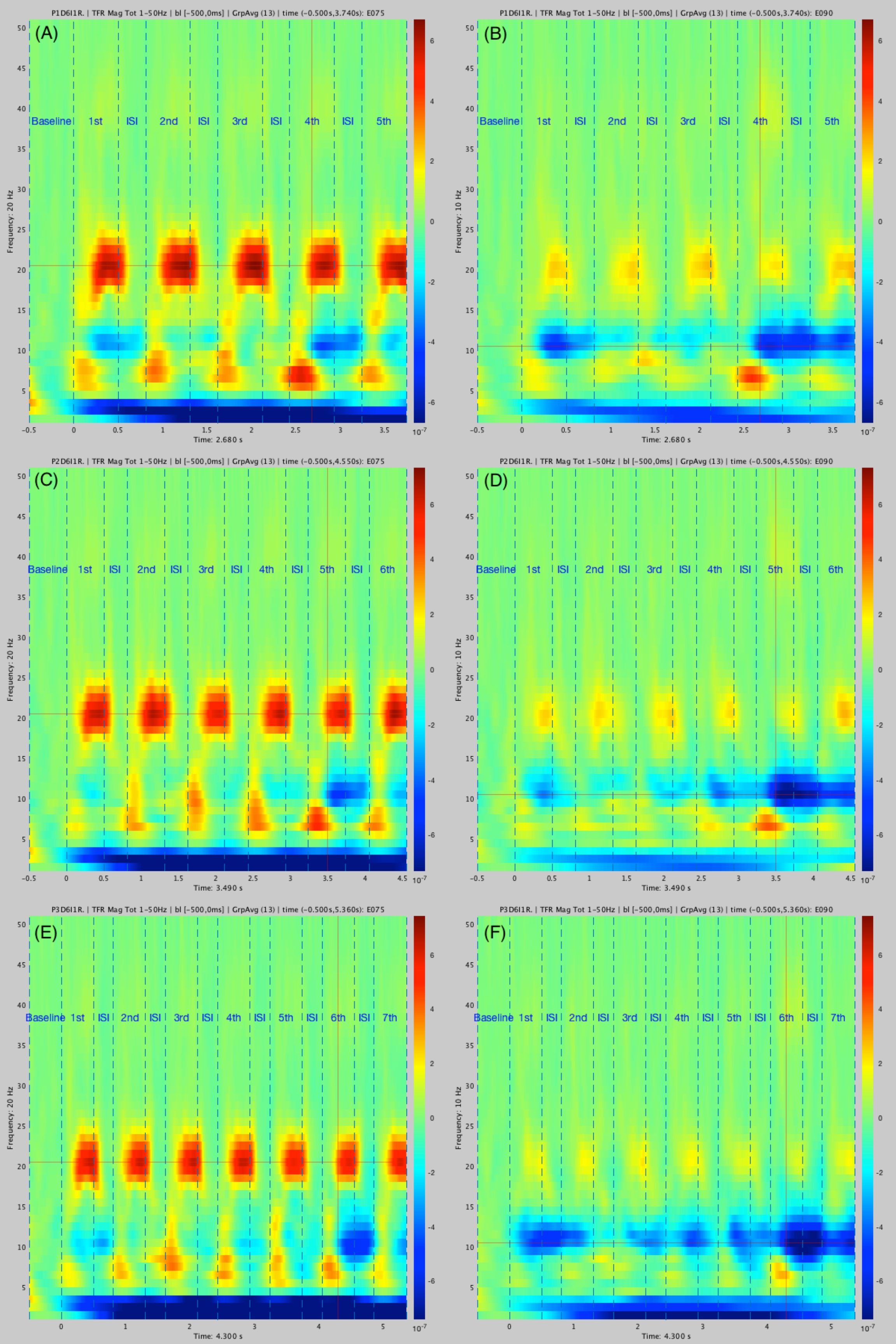
P1D6I1R. | TFR Mag Tot 1-50Hz | bl [-500,0ms] | GrpAvg (13) | time (-0.500s,3.740s): E075
(A)
Baseline 1st ISI 2nd ISI 3rd ISI 4th ISI 5th
Frequency: 20 Hz
Time: 2.680 s
P1D6I1R. | TFR Mag Tot 1-50Hz | bl [-500,0ms] | GrpAvg (13) | time (-0.500s,3.740s): E090
(B)
Baseline 1st ISI 2nd ISI 3rd ISI 4th ISI 5th
Frequency: 10 Hz
Time: 2.680 s
P2D6I1R. | TFR Mag Tot 1-50Hz | bl [-500,0ms] | GrpAvg (13) | time (-0.500s,4.550s): E075
(C)
Baseline 1st ISI 2nd ISI 3rd ISI 4th ISI 5th ISI 6th
Frequency: 20 Hz
Time: 3.490 s
P2D6I1R. | TFR Mag Tot 1-50Hz | bl [-500,0ms] | GrpAvg (13) | time (-0.500s,4.550s): E090
(D)
Baseline 1st ISI 2nd ISI 3rd ISI 4th ISI 5th ISI 6th
Frequency: 10 Hz
Time: 3.490 s
P3D6I1R. | TFR Mag Tot 1-50Hz | bl [-500,0ms] | GrpAvg (13) | time (-0.500s,5.360s): E075
(E)
Baseline 1st ISI 2nd ISI 3rd ISI 4th ISI 5th ISI 6th ISI 7th
Frequency: 20 Hz
Time: 4.300 s
P3D6I1R. | TFR Mag Tot 1-50Hz | bl [-500,0ms] | GrpAvg (13) | time (-0.500s,5.360s): E090
(F)
Baseline 1st ISI 2nd ISI 3rd ISI 4th ISI 5th ISI 6th ISI 7th
Frequency: 10 Hz
Time: 4.300 s
50 45 40 35 30 25 20 15 10 5
6 4 2 0 -2 -4 -6
10^{-7}

Fig 5.5. Single electrode TFR magnitude plots of Experiment 3.

The figure layout here is the same as that in Fig 5.3. The only difference is that the tagging frequency is 20 instead of 15 Hz. The data pattern is strikingly similar to that in Fig 5.3.

5.5 General Discussion

5.5.1 Main Findings

First, our study has first applied the SSVEP method for studying neural correlates of subsecond time perception. This is especially suitable for tasks with short (subsecond) inter-stimulus intervals, where the ERPs of each item tend to overlap with each other. Using EEG with SSVEP is especially advantageous for future time perception studies.

Second, the results were in favor of the attention enhancement hypothesis (New & Scholl, 2009; Tse et al., 2004) rather than the repetition suppression hypothesis (Cai, Eagleman, & Ma, 2015; Pariyadath & Eagleman, 2007, 2012; Schindel, Rowlands, & Arnold, 2011). The maximal alpha band magnitude decrement, which was associated with attention or temporal expectation in the literature (Gould, Rushworth, & Nobre, 2011; Kelly et al., 2006; Rohenkohl & Nobre, 2011; Sauseng et al., 2005), occurred specifically at the oddball. The repetition suppression theory (Eagleman & Pariyadath, 2009) specified that the first item and the odd item would have the largest neural response amplitude because they are immune from repetition suppression. However, this was not supported by our finding.

Third, the assumption of the repetition suppression theory (Eagleman & Pariyadath, 2009) that subjective duration corresponds directly to neural response amplitude may be less likely given our results. Although Sadeghi et al., (2011) did find linearly decreasing neural correlates of repetition suppression in the middle temporal visual cortex with fMRI, SSVEP has been shown in EEG to be a reliable measure of repetition suppression (e.g., Martens &

Gruber, 2012; Nemrodov, Jacques, & Rossion, 2015). Whether the discrepancy was due to the stimuli, the task, or the neural imaging tool awaits further studies.

5.5.2 Limitations

With SSVEP, one can easily argue that the neural correlates may not relate to the neural coding of perceived duration at all. For example, the TFR magnitude may reflect processes of visual flicker instead of duration. A more direct way to answer this question is to compare ERPs and TFRs between different subjective duration discrimination judgments. Alternatively, multivariate pattern analysis approaches can also be utilized to decode potential information contained in the SSVEPs. Nevertheless, the SSVEP method has been proven useful in identifying the neural correlates of visual perception, memory, and attention (for a review, see Norcia, 2015). Our contribution was to first apply this to subsecond time perception tasks. Future time perception studies can continue to exploit the high temporal precision of EEG and high signal-to-noise ratio of SSVEP to unravel time perception mechanisms.

In Experiment 1, although we have established that using the same tagging frequency for the standards and the oddball resulted to psychometric functions comparable to those with static stimuli, one cannot neglect the possible confounding of flicker-induced time dilation (e.g., Hashimoto & Yotsumoto, 2018; Herbst et al., 2013; Okajima, & Yotsumoto, 2016). It is likely that the amount of flicker-induced time dilation is similar for the standards and the oddball so as not to bias duration judgments in our experiments. Indeed, in our pilot studies, when the tagging frequency was different for the standards and the oddball, the PSE was affected by the frequency combinations. Therefore, it would be important to dissociate flicker-induced time dilation from the topic of interest if one were to apply SSVEP to time perception studies.

5.5.3 Future Directions

Consistent with Chapter II, attention is an important regulator of perceived duration. Connectivity analysis between electrodes that showed maximal alpha modulation during the oddball and all other electrodes may point to how attention regulates perceived time in terms of neural mechanisms. As SSVEPs of the visual stimuli are yoked to the physical timings, connectivity analysis can also be applied to the electrodes or sources of SSVEPs to reveal the processing stages of time perception.

5.6 Conclusions

Experiment 1 generalized the effect of subjective time expansion to flickering stimuli, making them suitable for frequency tagging of EEG data. This opens new possibilities for future time perception studies. Results in Experiments 2 and 3 are consistent with the attention enhancement (New & Scholl, 2009; Tse et al., 2004) but not the repetition suppression theory (Cai, Eagleman, & Ma, 2015; Pariyadath & Eagleman, 2007, 2012; Schindel, Rowlands, & Arnold, 2011). This further corroborates our findings and conclusions in Chapter II.

5.7 Acknowledgements

This work was supported by the National Science Foundation (NSF BCS-1439372), Japan Science and Technology Agency CREST, and Tamagawa-Caltech gCOE to Shinsuke Shimojo (principal investigator).

Commercial relationships: none.

Chapter VI

GENERAL DISCUSSION

6.1 Conclusions

Our findings achieved novel theoretical understanding of two specific time illusions: oddball chronostasis and debut chronostasis. The implications also provide new angles to the major debates of whether time perception arises from modality-independent or modality-dependent mechanisms (*research aim 1*, also see section 1.4.1), and whether time perception is mostly perceptual or cognitive in the hundreds of milliseconds range (*research aim 2*, also see section 1.4.2).

Chapter I reviewed major conceptual frameworks and findings in the field of time perception. We focused on the subsecond, hundreds of milliseconds range because the underlying mechanisms are not well-understood. Lewis and Miall (2003) suggested that the subsecond time perception mechanisms are more automatic, rather than cognitively controlled, based on their meta-analysis of previous time perception studies using positron emission tomography (PET) or fMRI. This almost entails that subsecond time perception mechanisms are more perceptual rather than cognitive. Therefore, our Research Aim 2 was to examine their proposal with psychophysical experiments on oddball (chapter II) and debut chronostasis (chapter III). Our Research Aim 1 was to tackle with a bigger issue—whether time perception is based on intra-, supra-modal mechanisms, or both. In order to achieve this, we challenged the findings of Rose and Summers (1995) that debut chronostasis is an illusion only in the visual modality, by testing whether debut chronostasis has similar strength in the intra-modality (visual-visual, auditory-auditory), and inter-modality (visual-auditory, auditory-visual) conditions (chapter IV). If time perception mechanisms are entirely supra-modal, then we expect similar illusion strength across intra- and inter-modal duration comparisons.

In Chapter II, our empirical data resolved disputes among three theories of oddball chronostasis since the initial report of debut chronostasis (Rose & Summers, 1995)—the attention theory (New & Scholl, 2009; Tse et al., 2004), the repetition suppression theory (Cai, Eagleman, & Ma, 2015; Pariyadath & Eagleman, 2007, 2012; Schindel, Rowlands, & Arnold, 2011) and the temporal preparation theory (Kim and McAuley, 2013). In Experiments 1 (digits) and 2 (orientations), we found that oddball chronostasis was explained half by top-down attention, half by saliency/adaptation, but not by prediction error. On top of that, temporal preparation but not repetition suppression explained why a later item appeared longer in duration. In Experiment 3 (colors), top-down attention was sufficient to explain oddball chronostasis; the outcome could not distinguish whether the modulatory effect by target serial position was due to temporal preparation or repetition suppression. Therefore, oddball chronostasis may be considered as a composite time illusion reflecting the coaction of three distinct mechanisms. The repetition suppression theory is overall less likely because its rival hypothesis, the temporal preparation theory, explains the item serial position effect even in a random item sequence, and because empirically, adaptation, a component of repetition suppression, is confounded with saliency. Thus, as far as Research Aim 1 (whether time perception mechanisms are modality dependent or independent) is concerned, the modality-independent view is more likely. This is because the inherent top-down attention factor is a modality-independent central mechanism (e.g. Tse et al., 2004) and because the empirically less supported repetition suppression is a modality-dependent process. As for Research Aim 2 (whether subsecond time perception are mainly perceptual or cognitive), we found that the mechanisms were mostly cognitive, given that top-down attention and temporal preparation are both cognitive while the repetition suppression hypothesis, which is basically perceptual, was at least partly ruled out (prediction error).

In Chapter III, we discovered a novel factor underlying debut chronostasis unaccountable by existing theories, and proposed a new hypothesis to explain the new findings. Noting that all previous debut chronostasis studies (Cai, Eagleman, & Ma, 2015; Pariyadath & Eagleman, 2007; Rose & Summers, 1995) set the first item as the target that varied in duration across trials and set the second or all the following ones as the constant reference, without testing the opposite, we added a novel condition where the second item was the target with variable duration and the first item was the reference with constant duration. In Experiment 1, debut chronostasis was largely reduced, if not nullified, in this novel condition. The repetition suppression hypothesis (Cai, Eagleman, & Ma, 2015; Pariyadath & Eagleman, 2007) could not explain this result because the average sensory memory traces did not change. Thus, two possibilities remained. One was the explicit instruction (a knowledge-based attention effect) on which item was the target; the other was the item uncertainty (variability) across trials. In Experiment 2, by keeping the instructions the same and varying the duration of the reference item instead, the results revealed that debut chronostasis was driven by item uncertainty but not explicit instruction. In both experiments, we also found that the duration uncertainty of the second and the third items did not lead to duration distortion at all. We think that these findings are in line with the theory (Morgan, Watamaniuk, & McKee, 2000; Nachmias, 2006) that the observers by default maintains an internal standard while performing judgment tasks. Our finding that in a four-item sequence, the uncertainty of the first item duration across trials elicits debut chronostasis is also novel in a broader literature context. In other duration discrimination studies using a two-item sequence, the presentation order of variable and constant items affected only discrimination sensitivity but not apparent duration (Bausenhart, Dyjas, & Ulrich, 2015; Dyjas, Bausenhart, & Ulrich, 2012; Hellström and Rammsayer, 2015; Lapid, Ulrich, & Rammsayer, 2008; Ulrich, 2010; Ulrich & Vorberg, 2009). This discrepancy deserves further investigation but basically may arose from confounding factors specifically in two-item paradigms such as the last item being perceived longer (Rose & Summers, 1995) and action preparation chronotasis (Hagura et al., 2012). Therefore, our results suggest that debut chronostasis may be a memory uncertainty effect. Thus, the critical question becomes whether this internal duration template is modality-dependent or independent. This chapter specifically addresses research aim 2, and suggests that subsecond time perception mechanisms are more cognitive (the internal duration template relies on the average of recent stimuli history) than perceptual (repetition suppression hypothesis is refuted).

In Chapter IV, we challenged the previous result that debut chronostasis occurs to vision but not to audition (Rose & Summers, 1995) and observed that auditory debut chronostasis also exists with comparable magnitude as visual debut chronostasis. By contrast, in the inter-modal conditions where a visual item was compared against an auditory item or the contrary, the average debut chronostasis was significantly lower than that in the intra-modal conditions. Therefore, this suggests that some time perception mechanisms exist at the intra-modal level. Then we swapped the order of variable and constant for the first two items as in Chapter III, and revealed that the modulation of the relative apparent duration between the first two items was a supra-modal effect. In other words, the reduction of debut chronostasis by keeping the duration of the first item constant across trials seems to be an additive effect on top of the intra- and inter-modal difference. Therefore, some time perception mechanisms also exist at the supra-modal level. This chapter specifically addresses research aim 1, and suggests that subsecond time perception mechanisms involve both intra- and supra-modal mechanisms.

All in all, for research aim 1, Chapter II and IV together support the idea that both intra- and supra-modal mechanisms exist for subsecond time perception; for research aim 2, Chapter II and III suggest that subsecond time perception is more cognitive than perceptual. As far as research aim 1 is concerned, unlike most theories that explicitly or implicitly postulate either a modality-dependent or independent view (for an overview, see Ivry & Schlerf, 2008), we propose that it is important for future theoretical developments to consider both intra- and supra-modal factors (and thus time perception mechanisms). This at least affects the influential theories that assume a modality-independent internal clock (Treisman, 1963; 1984), such as the scalar timing theory (Gibbon, Church, and Meck, 1984) and its neurobiological counterpart, the striatal-beat-frequency (SBF) theory (Matell and Meck, 2004), and other popular theories that assume modality-dependent coding of psychological time, such as the sensory cortex neural response amplitude assumption

(Eagleman and Pariyadath, 2009) accompanying the repetition suppression theory (Cai, Eagleman, & Ma, 2015; Pariyadath & Eagleman, 2007, 2012; Schindel, Rowlands, & Arnold, 2011), and the short-term synaptic plasticity model by Buonomano (2000). Recently, Merchant, Harrington, and Meck (2013) extended the core-timing mechanism concept and proposed that the central timing mechanism may interact with context-dependent areas, such as the primary sensory cortices or the cerebellum for perceptual and motor timing tasks. Whether this picture is true remains to be investigated, but at least performing more inter-modal timing experiments can be the next step towards explaining both psychophysical and neurobiological discoveries. As far as research aim 2, although in the meta-analysis of Lewis and Miall (2003), they interpreted that subsecond time perception recruits mostly automatic rather than cognitively controlled regions, our findings suggest that several cognitive factors (top-down attention, temporal preparation, and internal duration template) are already at play in the subsecond time range. Therefore, teasing apart the underlying factors with psychophysics could definitely help verifying interpretation of neural imaging results as well as lead to more critically designed experiments for neural imaging.

6.2 Limitations

In Chapter II, we pointed out that in the repetition suppression hypothesis, low-level adaptation is inseparable from saliency in all previous experimental designs including our own. It would be interesting to further distinguish between these two possibilities by proper experiments. For example, in the original oddball paradigm (the repeated sequence in Fig 2.1), there are only two types of singleton items: the standards and the oddball target. Each item is presented at the fovea one at a time. An idea is to embed the sequential singletons in a constant static surround full of task-irrelevant items either identical to the target or the standards. Target or standard, an item distinctively different from its simultaneous surround has higher saliency and will ‘pop-out’ so as to grab attention (e.g., Lagroix, Di Lollo, & Spalek, 2015). Thus, if constantly presenting a static surround identical to the oddball target weakened oddball chronostasis, the saliency hypothesis would be likely than the adaptation hypothesis, which further refutes the repetition suppression hypothesis; otherwise, the adaptation hypothesis would be favored over the saliency hypothesis.

In Chapter III, although we have shown that internal duration template uncertainty is a major factor in debut chronostasis. The repetition suppression hypothesis (Cai, Eagleman, & Ma, Pariyadath & Eagleman, 2007) may not have been entirely ruled out. In those two studies, debut chronostasis disappeared in an item sequence with random items. However, the identity of the first item was kept the same across conditions. As Chapter IV suggests, there could be an intra-modal stage of duration perception. It would be interesting to further carry out experiments to see if the internal duration template depends on modality-specific features at all. We could modify the four-item paradigm as the following. Utilize oriented bars as stimuli. All four items have the same visual attributes within trial, but from trial to trial, the orientation of the four bars change by a certain angle. Then we can analyze whether larger changes lead to larger uncertainty in internal duration template (hence larger debut chronostasis). If the answer were yes, then duration coding and visual coding would be at least partly mixed in the corresponding neural activity.

In Chapter IV, the number (8) of participants did not reach the expected number (15) in Experiment 2. For future publication purpose, it is imperative to gather more data, so that the additivity of intra- and supra-modal mechanisms can be further substantiated.

In Chapter V, at the time we finished the oddball chronostasis EEG experiments, we had not yet achieved the triple dissociation of the underlying mechanisms (top-down attention, saliency/adaptation, temporal preparation) yet. Therefore, the interpretations were limited at that time since we used only the repeated sequence. The ISIs were fixed to make EEG analyses simple, but introduced rhythm-based judgements as a confounding factor. Further, whether the neural signatures frequency-tagged by visual flicker reflected flicker itself rather than time perception was a confounding that could be ruled out by future control experiments.

Overall, besides the distinction between intra- and supra-modal mechanisms, there is an alternative viewpoint based on inter-modal mechanisms. In other words, what is believed to be intra-modal mechanisms (e.g., sensory cortex neural dynamics) could a result of inter-modal mechanisms (e.g., functional connectivity between the visual and auditory areas) in disguise. Neural imaging may be the best tool for tackling this type of issue.

6.3 Future Directions

One future direction is to quantitatively examine how the time perception factors revealed in this dissertation are a function of standard/reference duration, given that the standard duration was fixed at 500 or 600 ms in all experiments of this dissertation. For example, Tse and colleagues (2004) have tested this aspect of the attention theory and found a nonlinear function of attention effect that depends on the standard duration. That nonlinear pattern matches earlier studies on the transient and sustained components of attention (e.g., Nakayama & Mackeben, 1989; Remington, Johnston, & Yantis, 1992). Some effects could be independent of the standard duration and linearly additive to other co-existing effects; others could be proportional to the standard duration. For example, the influential scalar timing theory by Gibbon et al. (1984) attributes linear additive effects to the switch component and multiplicative effects to the clock or the memory components. Currently, the mechanisms of interest include top-down attention, saliency/adaptation, and temporal preparation from oddball chronostasis, as well as the internal duration template from debut chronostasis. The results will be informative for future computational models.

Since Chapter IV suggested that both modality-independent and modality-dependent time perception mechanisms exist, an important direction is to carry out neural imaging studies to localize each mechanism identified by our psychophysical studies. This will further reveal the neural signatures of subjective time. Specifically, connectivity analysis would be helpful in understanding how the modality-dependent and modality-independent stages are functionally linked.

In terms of neural correlates of time perception, previous fMRI and EEG studies provided some valuable clues of time perception mechanisms. With fMRI, previous research has shown a highly distributive nature of cortical and subcortical areas across different studies, where SMA and rIFG are common across perceptual and motor timing studies (for a review, see Wiener, Turkeltaub, & Coslett, 2010). With EEG, the best neural correlates of timing and time perception was contingent negative variation (CNV) first reported by Walter, Cooper, Aldridge, McCallum, and Winter (1964). Using a paradigm with a warning signal and an imperative stimulus, participants were required to prepare to perform a button press upon the onset of the warning signal and do so upon the onset of the imperative stimulus. They found that between the warning signal and the imperative stimulus onsets, there was a sustained gradual negative component most prominent in the frontal-central electrodes, named CNV. So far, an unambiguous interpretation of CNV remains elusive. Kononowicz and Penney (2016) summarized that CNV could be a composite event-related potential (ERP) component that mixes working memory, preparation, and anticipation effects. Since subsecond time perception is relatively brief, a promising direction could be to identify the neural dynamics and transient connectivity between CNV and other modality-specific ERP components by EEG. We would like to address these possibilities in future studies.

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