

**Pupillometry and time perception:
Temporal modulation caused by pupillary light reflex to
luminance-controlled stimuli**

(輝度統制刺激が誘発する対光反射に伴う知覚時間変調)

January 2023

Doctor of Philosophy (Engineering)

Yuya Kinzuka

金塚 裕也

Toyohashi University of Technology

Date of Submission (month day, year) : January 6th, 2023

Department of Computer Science and Engineering		Student ID Number	D163326	Supervisors	Shigeki Nakauchi Tetsuto Minami
Applicant's name	Yuya Kinzuka				

Abstract (Doctor)

Title of Thesis	Pupillometry and time perception: Temporal modulation caused by pupillary light reflex to luminance-controlled stimuli
-----------------	--

Approx. 800 words

Temporal perception and the ability to precisely ascertain time duration are central to essentially all behaviors. Nevertheless, humans do not have a dedicated receptor that can directly perceive the flow of time and believed that our brain creates a subjective sense of time by integrating various endogenous and sensory inputs. Therefore, our perception of time can be influenced by various non-temporal aspects of the stimulus, known as the “temporal distortion.” Interestingly, the pioneering works on temporal perception have consistently found that the subjective duration of a given interval generally correlates positively with the magnitude of the stimulus (“more-is-longer” account). These studies have reported the occurrence of temporal distortion due to non-temporal factors related to the physical aspect of the stimulus, using temporal perception tasks with stimuli associated with different sensory inputs. However, stimulus magnitude can be determined by a complex interaction of the physical intensity, internal representation, and even by pupillary responses of the stimulus. In other words, temporal distortion effect may vary depending on the equiluminant method used. It is important to further clarify the involvement of these factors, especially since the effect of color and luminosity on temporal perception—the most well-known non-temporal aspects that can cause temporal distortion—is still a topic of controversy. In this thesis, we conducted a series of temporal perception experiments to evaluate the effects of different representations of stimulus magnitude on temporal perception, and the role of pupillometry in temporal distortion. Three research questions were addressed in this study.

In the first study, we used color stimuli as the to-be-timed target to answer two research questions: 1) what is the potential effect of color (specifically red versus blue) on temporal perception under different intensity matching conditions, and 2) what is the relationship between pupillary response and temporal perception? Results from previous studies on the perceived duration of red versus blue have been inconsistent since the 1960s, which may be due to difficulties in controlling physical properties such as hue and luminance within and between studies. Therefore, we conducted a two-interval duration-discrimination task to evaluate the perceived duration of color stimuli under different equiluminant conditions: subjective equiluminance and pupillary light reflex (PLR)-based equiluminance. The results, based on psychometric functional analyses and simultaneous pupillary recordings, showed that the perceived duration of red was overestimated compared to blue even when the intensity was

controlled based on subjective equiluminance. However, since blue is known to induce a larger PLR than red despite equiluminance, we conducted a controlled study to differentiate the indirect effect of pupillary response on temporal perception. Interestingly, the effect observed in the first experiment faded when the luminance levels of the two stimuli were matched based on PLR response. These results indicate that duration judgment can be influenced not only by the hue but also by different equiluminance methods.

In the second series of experiments, we adapted an optical illusion named the glare illusion, which enhances the perceived brightness without any actual change in physical intensity, as the to-be-timed target during pupillary recording. This paradigm enabled us to explore two research questions: 1) is subjective magnitude itself sufficient to induce temporal illusions when physical intensity is identical, and again, 2) what is the relationship between pupillary response and temporal perception? This is because it remains unclear how perceptual magnitude, which is assumed to link temporal perception itself directly affects temporal perception. Therefore, we again conducted a duration-discrimination task using glare, halo, and glare-equivalent stimuli. Based on the mean difference in the point of subjective equality derived from a psychometric function and pupil diameter, we found that temporal perception is influenced by the illusory brightness of glare stimuli. Interestingly, the perceived duration of the apparently brighter stimuli (glare stimuli; larger PLR) was shorter than that of control stimuli (halo stimuli; smaller PLR) despite the stimuli remaining physically equiluminant, in contrast with the well-known “more-is-longer” account. Furthermore, this temporal modulation did not occur when the physical luminance of the stimuli was manipulated to match the illusory-induced magnitude. These results indicate that temporal processing depends on the confluence of both external and perceived subjective magnitude, and even illusory brightness is sufficient to affect the sense of duration; which may be explained by the internal magnitude decrease of the glare stimuli due to pupillary constriction decreasing the light entering the eye.

We believe this study not only provides the fact what/which stimuli is perceived subjectively longer but also provides new insights into the importance of what equiluminant methods to use. Furthermore, the fact that PLR amplitude matching resulted in the fading of temporal distortion suggests a new perspective for future studies. While there are currently no physiological models suggesting a differential effect of different PLR amplitudes on temporal perception, our finding of a causal relationship between PLR matching and temporal distortion effects can be explained by neural intensity fluctuations based on the amount of light entering the pupil and the coding efficiency model. Further considerations incorporating psychology, optical, and neuroscience approaches will be required to yield further discussion on theoretical frameworks and the probable mechanism, which should provide an important clue to elucidate the underlying mechanism of temporal perception in humans.

Acknowledgments

Time flies when you are in exciting moments.

So, no wonder my PhD journey has passed by in a blink.

Undertaking this PhD has been a truly life-changing experience for me, which would not have been possible without the exceptional support and guidance of many people. This is why I would like to dedicate several pages of my thesis to express my deepest gratitude to all. First and foremost, I would sincerely would like to give my special regards to my supervisor, Prof. Shigeki Nakauchi, for his continuous support and meaningful discussions. If it were not for him, I would definitely not have decided to continue my progression in the field of cognitive science and psychophysics in the doctoral course, and would not be able to open my eyes to the fun of science and research. That is why I would like to thank him again for convincing and encouraging me (and even my father over the phone), when I was sitting on the fence about my decision to pursue my dream, the progress toward the Phd course.

I would also like to sincerely appreciate my esteemed supervisor, Prof. Tetsuto Minami, for providing his expertise and innovative ideas that greatly assisted in conducting the research. Moreover, the day-to-day conversations with him in the “Dr-room” and his friendly personality made it possible to live my student life by being myself. In addition, I will also never forget his and his family’s hospitality during my time in Oslo, Norway, which remains one of my fondest memories from my student years. It is a great honor to have had numerous opportunities to be a part of amazing experiences with these two professors. I also wish to show my gratitude to Kyoko Hine and Hideki Tamura, assistant professors in the Department of Computer Science and Engineering who supported me during the research period by providing innovative ideas during weekly staff-meetings.

I am fortunate to have been one of the students that was able to get involved in many of their joint research projects and business trips. Without the inclusive support of Prof. Shigeki Nakauchi, Prof. Tetsuto Minami, and Asst.Prof. Kyoko Hine and Asst.Prof. Hideki Tamura, this PhD study would not have been achievable. In addition, I would like to thank Prof. Michiteru Kitazaki for evaluating this study with scrupulous attention. It was a great honor to be treated equally as a fellow researcher and not just as a student by all the members.

Additionally, I wish to express my deepest gratitude to Ms. Yuki Kawai, secretary of the Visual Perception and Cognition Laboratory, for supporting me during the six years of my student life in Toyohashi. She provided me with a lot of valuable advice that assisted me in living a healthy and productive student life. I will miss the early-morning “chit-chats” with her in the M1-room, which were like an oasis for the mind. In addition, I deeply thank Prof. Bruno Laeng, University of Oslo, for providing valuable advice regarding pupillometry since long ago and supporting my visit to Norway. I really appreciate his words of encouragement about challenging myself and advancing in the doctoral course, sometimes by even (humorously) quoting Shakespeare’s words. Along with his support in Oslo, I also would like to give my regards to *RITMO, the Centre for Interdisciplinary Studies in Rhythm, Time and Motion*, and *RITPART* (project number 274996) partner institutions for providing the opportunity to conduct studies in Oslo that broadened my perspective.

I would also like to thank Dr. Fumiaki Sato for his enthusiastic guidance and contribution to many of my studies. It was an honor to have a mutual research interest in temporal perception and pupillometry, and to discuss (or sometimes even challenge one another) on the probable underlying mechanisms of my research study. In the same context, I thank all my research unit members of the Visual Perception and Cognition Laboratory as well as the Cognitive Neuro-technology Laboratory for the meaningful discussions we have had. It was a big pleasure being the leader of one of the largest research units in the Laboratory. I have also learned a lot through the guidance to the junior students.

Furthermore, I would like to thank Yuma Taniyama, for overcoming the difficult times we faced together as a result of our healthy rivalry. We both may have had moments where we felt some sense of inferiority by realizing what the other had, and what we didn’t have individually. However, I believe those moments were important to grow as individuals, and I simply enjoyed the discussions we had on various topics. Honestly, I’m very happy that we could (hopefully) graduate together! I appreciate the other graduated seniors and research fellows with whom I got acquainted with during the lab assignments, because this research would not have been possible without overcoming the challenging period together.

I hope I haven't skipped someone, but even if I did, everyone reading this thesis should be important to me; and please know that I am very grateful for your support.

This thesis was supported by the Grants-in-Aid for Scientific Research (KAKENHI), Grant Number: JP21J12728, from the Japan Society for the Promotion of Science (JSPS). In addition, the JSPS Research Fellowships for Young Scientists (JSPS DC) have financially supported my student life.

Finally, I would also like to say a heartfelt thank you to my parents for supporting me financially and providing the opportunity to study away from my hometown. Even more, I thank them for respecting my decision of the progression to the doctoral course (and maybe for not asking how much longer it was going to take me to finish it). And finally, to my wife, who has been by my side throughout this PhD journey. Balancing work, research studies, and private life was not easy, especially because of time constraints. Time is finite. There were many days I had to stay up late to finish some work or got pre-occupied by research matters. Therefore, I am very grateful for her support and understanding, which made it possible for me to complete what I had started.

Contents

Chapter 1	Introduction	1
1.1	Time: an important dimension of perception	1
1.2	The relativity of time	2
1.3	Background and Aim	3
1.4	Research questions	5
1.5	Structure of thesis	6
Chapter 2	Related studies	9
2.1	Perceptual time and temporal distortion	9
2.2	Temporal experiment tasks	11
2.2.1	Bisection task	12
2.2.2	Duration discrimination (comparison) task	12
2.2.3	Generalization task	12
2.3	Evaluation of the perceived duration	13
2.3.1	Proportions of “long” responses	13
2.3.2	Point of subjective equality (PSE)	14
2.3.3	Just noticeable difference (JND)	15
2.4	Theoretical accounts	16
2.4.1	Internal-clock principal / pacemaker-accumulator model	16
2.4.2	Coding efficiency model	16
2.5	Psychological studies on the functioning of Red/Blue	18
2.6	Color to temporal perception	20
2.7	Brightness to temporal perception	22
2.8	Pupillary light reflex	23
2.9	Pupil and temporal perception	25
Chapter 3	Hypothesis Testing: The effect of Red/Blue on temporal perception and pupillary	

	response induced by different equiluminant conditions	27
3.1	Red longer? or blue longer?	27
3.2	Subjectively equiluminant condition (Experiment 1)	30
3.2.1	Introduction	30
3.2.2	Materials and methods	30
	Participants	30
	Stimuli and apparatus	30
	Procedure	31
	Data analysis	33
3.2.3	Results	34
	Adjustment task	34
	Duration judgment	34
	Pupillary response	36
3.2.4	Discussion	37
3.3	PLR-matched condition (Experiment 2)	40
3.3.1	Introduction	40
3.3.2	Materials and methods	40
	Participants	40
	Stimuli and apparatus	40
	Procedure	41
	Data analysis	41
3.3.3	Results	42
	PLR-matching task	42
	Pupillary response	43
	Duration judgment	44
3.3.4	Discussion	46
3.4	Discussion	47
Chapter 4	The effect of glare illusion-induced perceptual brightness on temporal perception	55
4.1	Introduction	55
4.2	Illusory magnitude on temporal perception (Experiment 1)	59
4.2.1	Introduction	59
4.2.2	Materials and methods	59

	Participants	59
	Stimuli and apparatus	60
	Procedure	61
	Data analysis	63
4.2.3	Results	64
	Duration judgment	64
	Pupillary response	65
	Mediation analysis	68
4.2.4	Discussion	69
4.3	Illusory magnitude matched (Experiment 2)	70
4.3.1	Introduction	70
4.3.2	Materials and methods	70
	Participants	70
	Stimuli and apparatus	70
	Procedure	71
	Data analysis	72
4.3.3	Results	72
4.3.4	Discussion	72
4.4	Discussion	74
Chapter 5	Conclusion	79
5.1	Summary	79
5.2	General discussion	80
	Publication List	85
	Bibliography	87

List of Figures

1.1.1	The dimension of time?	1
1.5.1	Thesis structure	7
2.1.1	The relationship between the temporal distortion effect and the internal clock	10
2.3.1	An example psychometric functions with a different point of subjective equality (PSE) .	14
2.3.2	An example psychometric functions with a different just noticeable difference (JND) . .	15
2.4.1	A generic pacemaker-accumulator model	17
2.8.1	Neuronal control of the PLR	24
3.2.1	Experimental protocol for one trial (Exp.1 & Exp.2)	32
3.2.2	Histogram and distribution fit of the adjusted Y-values	35
3.2.3	Mean psychometric functions (subjective equiluminance)	36
3.2.4	Mean PSE of each color sequence	37
3.2.5	Pupillary response to each color stimulus (subjective equiluminance)	38
3.3.1	Example pupillary response and peak PLR amplitude	42
3.3.2	Histogram and distribution fit of the calculated Y-values	43
3.3.3	Pupillary response to each color stimulus (PLR-based equiluminance)	44
3.3.4	Mean psychometric functions (PLR-based equiluminance)	45
4.1.1	The Ebbinghaus illusion (Titchener circles)	56
4.1.2	Glare and Halo stimuli	58
4.2.1	Experimental protocol for one trial (Exp.1 & Exp.2)	62
4.2.2	Mean psychometric functions (illusory condition)	65
4.2.3	Mean psychophysical function properties (illusory condition)	66
4.2.4	Pupillary response to glare and halo stimulus	67
4.2.5	Schematic diagram of mediation analysis results	68
4.3.1	Mean adjusted luminance equivalent to glare/halo stimulus	73

4.3.2	Mean psychophysical function properties (illusory-magnitude matched condition)	. . .	74
-------	--	-------	----

List of Tables

2.6.1	Summaries of studies on red/blue on time perception	21
3.4.1	Descriptive results table of the PSE in both Color and Exp condition	48
3.4.2	Two-way repeated-measures ANOVA table on the effect of the PSE	49
3.4.3	Simple main effects on Exp condition	49
3.4.4	Simple main effects on Color condition	49
3.4.5	Post-hoc comparisons result for $\text{Exp} \times \text{Color}$ condition	50
4.2.1	Two-way repeated-measures ANOVA table on the effect of the PLR amplitude	67
4.2.2	Mediation analysis result - parameter estimates	69
5.2.1	Summary of the studies	81

1 | Introduction

1.1 Time: an important dimension of perception



Fig. 1.1.1: The dimension of time?

A time-lapse scenery photo captured from the window of the author's lab. This composition serves as a reminder that photographs can capture moments that are irreversible, with each moment being distinct and unique from the last. Time is not a coordinate in the context of relativity; instead, it is the dimension itself that contains the "position" of each moment.

The concept of time in humans is regarded to be already born in the 1500s BCE. after the discovery of a simple sundial by the ancient Egyptians. For millennia, humans have been measuring time in various ways, and with the spread of mechanical watches, the unfettered lapse of permanent time has changed into aspects of constrictions. With the establishment of social order and the progress of globalization, not a single day goes by without being conscious of the time: Time truly is ubiquitous. We understand time

is some kind of a continuous sequence of events that take place in apparently irreversible succession from the past to the future, as a definition. However, compared to other “tangible” dimensions of perception, such as depth, shape, movement, visual, auditory, olfactory, and various other fields, the dimension of times seems to be impalpable and sometimes even conveys vague anxiety to the public when researchers refer to the term “temporal perception.”

1.2 The relativity of time

An old newspaper article published in the New York Times has reported that Albert Einstein told his secretary to answer: *“When you sit with a nice girl for two hours, you think it’s only a minute; But when you sit on a hot stove for a minute, you think it’s two hours. That’s relativity.”* when she is bothered by inquisitive interviewers, who wanted to know what relativity really meant (TIMES~, 1929). Although this quote was used to explain the abstruse theory of relativity (Einstein, 1929/2011), this quote also reflects the ambiguity of subjective time experience. In other words, the perceptual time is not isomorphic to the physical time, as understood from our own personal experiences. Time seems to fly when we are having fun and drags when we are bored; a return trip feels much shorter than the initial outbound way, and time passes faster as we age. This exhibits that non-temporal factors such as emotions, experiences, and our internal states dramatically influence our subjective experience with regards to the passage of time. Although time can be measured in objective standardized units, humans have no specific receptor to directly perceive time flow, and neither do they have any mechanism to produce an accurate pulse, such as the quartz resonators observed in digital clocks (Muller and Nobre, 2014).

Nevertheless, the perception of time is fundamental to our daily lives and the ability to precisely time the duration of temporal intervals is central to all essential behaviors; from basic behavioral controls such as foraging and communication, to unique human activities such as deciding whether to click the “back button” on a slow-loading web page or waiting for a cup of instant noodles that is optimally prepared in 3 minutes. Humans are constantly engaged in various mental and physical activities under the constraints of time. Consequently, temporal perception has been a focus of research since the early days of experimental psychology (James et al., 1890; Myers, 1971; Grondin, 2010), which led some studies to focus on developing quantitative models of temporal perception that are grounded in neurobiology. This was done by investigating sense organs which might be dedicated to time and by looking for the responsible brain regions. Although several models of subjective temporal modulation have been proposed, the underlying neuronal mechanism still remains unclear (Matthews and Meck, 2016).

Subsequently, the perception of time is a fundamental function that permeates all sensory, motor, and cognitive processes. The clarification of the temporal perception mechanism may even lead to the elucidation of interdisciplinary studies such as the tachypsychia phenomenon in which the perceived time lengthens, making events appear to slow down during intense physical exertion such as car accidents and explain the “flow state” which is a mental state of operation during times of extreme concentration and full involvement. Moreover, as athletes with high physical abilities occasionally acquire a “zone” experience by training, the clarification will also help elucidate how far humans can interfere with the dimension of time as well as its limitations.

1.3 Background and Aim

Color, which is a measure of hue, chroma, and saturation, and luminance (a measure of light), are both also ubiquitous to our perception of the world. Color vision processing in the human visual system is initiated by the absorption of light by three different types of cone photoreceptors with distinct absorption spectra and the rod photoreceptor (Grimes et al., 2018). This means that the stimuli’s luminance (intensity) and color (wavelength) are ambiguous to the responses of a single photoreceptor. Hence, the color and brightness perception rely on comparing the relative activities of all types of photoreceptors (Rushton, 1972).

Given the considerable growth of research in the field of human vision and temporal perception, psychophysical or behavioral techniques have been employed to reveal how non-temporal information modulates the subjective perception of time. In many previous studies, stimuli with different visual sensory input were used to investigate how the apparent duration of a time interval is influenced (in other words, how temporal illusions occur) by low-order characteristics such as color and brightness. Despite the fact that mechanisms causing temporal illusions remain unclear, temporal illusions are known to occur when the subjectively perceived time duration does not faithfully represent its physical duration of an interval, which is assumed to be positively related to the magnitude of the stimuli (Eagleman, 2008; Rammsayer and Verner, 2014; Walsh, 2003) (*e.g.*, brightness, size, arousal induced by the stimuli). This is one reason why the aspects of color and brightness on temporal illusion have been intensively reviewed for decades (*e.g.*, Smets, 1969; Goldstone and Goldfarb, 1964; Goldstone et al., 1978).

For instance, Smets was the first to suggest the potential effects of color on temporal perception (Smets, 1969). Smets continuously exposed participants to red and blue lights continuously for 45 s. Subsequently to the exposure, participants verbally reported the estimated duration of each color presentation. The

result exhibited that the duration of blue stimuli was overestimated in comparison to red stimuli (blue was perceived longer than red). In the same way, many previous studies instructed participants to respond to the duration of the red/blue stimuli by either a temporal bisection task or a duration discrimination task (see section 2.2 for further information). The derived mean point of subjective equality (“PSE”) was then compared to examine the temporal modulation. Recently, Shibasaki et al. reported that the red stimuli were perceived to be significantly longer after comparing the subjective temporal perception of red/blue stimuli (Shibasaki and Masataka, 2014). Contrary to this study’s result, Thönes et al. reported a temporal overestimation in the blue stimuli compared to red (Thönes et al., 2018).

Assuming that hue also plays a vital role in the distortion of perceived time, it is clear that other physical aspects of the color such as brightness and saturation, should be taken into consideration besides the hue of the color stimulus since temporal illusions are known to occur by the intensity received from the stimuli (Eagleman, 2008; Walsh, 2003) and simply by the luminance of the stimuli (Goldstone and Goldfarb, 1964; Goldstone et al., 1978; Brigner, 1986). Furthermore, some studies suggest that even the subjective brightness of the stimuli can cause temporal modulation (Casini and Macar, 1997). As a matter of fact, the brightness of the stimuli used by Smets was matched based on the apparent luminosity, however, failed to control the saturation of each stimulus (Smets, 1969). Even more, as we focus on the physical properties used in the red/blue temporal perception studies, some recent studies (Shibasaki and Masataka, 2014; Gorn et al., 2004) have used the primary colors, which will result in a different physical luminosity and saturation. Additionally, the color properties of the stimuli pair in the overall previous study, are mostly unique and matched based on different equiluminant or control methods. Although the time modulation induced by these color stimuli has been studied for more than 50 years, the underlying mechanism has not been sufficiently investigated when the fact, “which color results in time dilation?” is still controversial. These inconsistent results on the effect of color on temporal perception may be attributed to the lack of control over physical properties such as the luminance of the visual stimuli.

Moreover, aside from physical properties, physiological aspects such as the pupillary response may require consideration when discussing the temporal modulation by the stimulus’ hue. This arises from the fact that different hue evoke different pupillary light reflex (PLR), even at identical physical luminance (*e.g.*, Szabadi, 2012; Janisse, 1977; Wardhani et al., 2022). Since the PLR is driven by known photoreceptors, such as rods, cones, and intrinsically photosensitive retinal ganglion cells (ipRGCs) (Markwell et al., 2010), all of which have different sensitivity characteristics (Mathôt, 2018), short-wavelength light (blue) is known to induce more sustained PLR compared to long-wavelength light (red) (Szabadi, 2012; Herbst et al., 2011; Young and Kimura, 2008). Due to the inseparable interaction of physical properties

and pupillary responses, controlling methods can largely influence the principal results. To elucidate the underlying mechanism of temporal perception in humans, it is important to clarify this inconsistent relation of color and temporal perception.

To overcome these limitations raised by inconsistent results on the effect of color in relation to temporal perception, this thesis first focused on the stimuli equiluminance and controlling the physical aspects of the stimuli. Although equiluminance can be defined literally as “equally luminant,” the luminance of the stimuli can be matched in several ways: physical luminance, subjective (perceptual) luminance, and PLR based on the intensity match. By controlling the differences of the luminance in red/blue stimuli, the perceived interval duration was measured by a temporal task to examine the potential effect of color on temporal modulation. Simultaneously, the pupil diameter recording was combined with the study for two reasons: PLR matching and the investigation of the relationship between the pupillary response and temporal perception. In addition, the perceived interval duration of a visual stimulus whose perceived brightness was altered by the illusory effect was measured while undergoing pupillary response recording as an index of perceptual brightness. This was to examine whether temporal modulation can occur not by the physical magnitude difference, but by the subjective magnitude difference of the stimuli and different pupillary responses. These approaches should contribute to the elucidation of the underlying mechanism of temporal illusions. Focusing on the connection between pupillary responses and the temporal perception could provide a hint to uniformly explain the inconsistent research findings.

1.4 Research questions

In this thesis, we described a series of experiments to evaluate the effects of various representations of stimulus magnitude on temporal perception by focusing on the most renowned non-temporal aspects that induce the temporal distortion: color and luminosity. In addition, pupillometry was combined with the experiment for the purpose of PLR matching and to see how pupillary responses are involved in temporal distortion. This thesis addresses three research questions with respect to the various representations of stimulus magnitude and the involvement of pupillometry in temporal perception, as described below:

Research question 1: What is the potential effect of color (especially red v.s. blue) on temporal perception under careful stimuli control? Will different equiluminant methods result in different temporal illusions? If so, what is the causal mechanism?

Research question 2: Is subjective magnitude itself sufficient to induce temporal illusions when the

physical intensity is identical? In other words, does temporal processing depend on the confluence of both external magnitude and perceived subjective magnitude?

Research question 3: What is the relationship between pupillary response and temporal perception? Can pupil diameter be an index for subjective temporal perception? Or does the pupil size affect temporal perception?

1.5 Structure of thesis

Figure 1.5.1 exhibits an outline of this thesis, comprising five chapters. Related studies on temporal perception and experimental methods used in the main study are mentioned in chapter 2. In this thesis, we conducted a series of temporal perception experiments to evaluate the effects of different representations of stimulus magnitude on temporal perception, and the role of pupillometry in temporal distortion. In chapter 3 and 4, an investigation of the potential effect of color and luminance on temporal perception by temporal experiments are mentioned, both comprising general discussions in relation to the relationship between pupillary response and temporal perception. Each series of study focused on the temporal distortion effect based on the aspect of equiluminant conditions. Finally, the overall summary of the studies and answers to the research questions are mentioned in chapter 5.

Introduction

Background

Human has no specific receptor that can directly perceive the flow of time. Persistent studies on temporal distortions effect have generally indicated that the subjective duration of time correlates positively with the to-be-timed stimulus magnitude. However, stimulus magnitude can be determined by the complex interaction of the physical intensity, internal representation, and pupillary responses of/to the stimuli. The involvement of these factors needs further clarification, especially when the effect of color and illusory brightness on temporal perception is still a topic of controversy.

Research questions

RQ.1: What is the potential effect of color (especially red v.s. blue) on temporal perception under careful stimuli control?

Will different equiluminant methods result in different temporal distortion effects?

RQ.2: Is subjective magnitude itself sufficient to induce temporal illusions when physical intensity is identical?

RQ.3: What is the relationship between pupillary response and temporal perception?

Chapter 1

Related studies

Perceptual time and temporal distortion

Theoretical accounts

Color to temporal perception

Brightness to temporal perception

Pupillary light reflex

Pupil and temporal perception

Chapter 2

Body

Red/Blue Study

Main focus on *RQ.1* and *RQ.3*

Connection between equiluminant methods and temporal perception

The effects of equiluminant color on temporal perception was evaluated by a two-interval duration discrimination task.

Experiment 1

- The magnitude of the two color stimuli was matched subjectively; however was also physically equaluminant.
- Red stimuli were temporally overestimated compared with the blue stimuli.
- The PLR (pupillary light reflex) amplitude significantly differed by the hue of the stimuli.

Experiment 2

- Stimuli intensity was matched individually based on the PLR amplitude.
- In contrast to Exp.1, statistical analysis suggests no significant temporal distortion by the hue condition.

The results suggest that the pupillary response plays a role in temporal perception from a phenomenological perspective. This causality between equiluminant methods and temporal distortion effect may be mediated by the amount of incident light entering the pupil, leading to different degrees of neural activation in visual-related regions.

Chapter 3

Glare/Halo Study

Main focus on *RQ.2* and *RQ.3*

Effect of illusory magnitude on temporal perception

The main procedure of the experiments was identical to the Red/Blue study, except for the to-be-timed stimuli.

Experiment 1

- An optical illusion was used for the to-be-timed target to examine whether temporal distortions occur by stimuli with physically identical intensity while perceptual brightness differs.
- Temporal distortion also occurred by illusory brightness. However, on the contrary to the well known “more-is-longer” account, the glare stimuli (apparently brighter; larger PLR) was perceived shorter.

Experiment 2

- Temporal distortion effect faded When the stimuli were replaced with illusion-equivalent uniform stimuli.

The results indicate that temporal processing depends on the confluence of both external magnitude and perceived subjective magnitude. Also, the probable mechanism of the temporal distortion can be explained by a causal relationship between glare illusion-induced pupil constriction, activation amount and the coding efficiency model.

Chapter 4

General discussion & Conclusion

Based on the analysis of psychometric functions and pupil diameter in a series of studies, results suggest that different equaluminant methods can result in different temporal modulation. Furthermore, from a phenomenological perspective, this causal relationship can be explained by the stimuli-induced constriction amount in pupil size.

RQ.1: The perceived duration of red was longer than blue, even when the physical aspects of the stimuli were controlled. This result not just provides the fact which is longer but also raise the importance of what equiluminant methods to use.

RQ.2: Illusory brightness is sufficient to induce temporal distortion. This also mean that perceptual representations of the magnitude, which is assumed to link temporal perception, depend on the confluence of external and internal processing.

RQ.3: In the context of the coding efficiency model, pupil size seems to affect temporal perception by neural intensity fluctuations based on the amount of incident light entering the pupil and not vice versa.

Chapter 5

Fig. 1.5.1: Thesis structure

2 | Related studies

2.1 Perceptual time and temporal distortion

Time is a fundamental dimension that pervades all sensory and cognitive processes. From a physicist's viewpoint, time is considered a spatial dimension that represents the change or a relative position in a gravitational field which can be measured in objective standardized units. As opposed to physical time, perceptual time cannot be measured in objective standardized units, and the sense of time is a universal, continuous experience. Unlike other basic dimensions, human has no specific receptor that can directly perceive the flow of time ([Matthews and Meck, 2016](#)), which means that perceptual time can significantly differ between different individuals and/or in different circumstances. This has led to temporal perception often being studied and discussed in relative isolation.

This phenomenon, in which the perceived duration of time does not faithfully represent the physical duration, is frequently called the temporal distortion or temporal illusion (*e.g.*, [Matthews and Meck, 2016](#); [Arstila and Lloyd, 2014](#); [Pande and Pati, 2010](#)). In such cases, a person may momentarily overestimate or underestimate the physical duration as depicted in Figure 2.1.1.

Since the pioneering works on temporal perception, it is known that our perceptual time is affected by both internal and external factors ([Hoagland, 1933](#); [Gil and Droit-Volet, 2011](#)). These factors include metabolism, emotions such as arousal and valence, and other external non-temporal factors that may affect individuals' internal states. In this section, we will summarize some previous studies showing various non-temporal aspects of the stimulus influence and its apparent duration (see ([Matthews and Meck, 2016](#)) for a detailed review). Goldstone et al. presented a pure tone stimulus in different intensities (64 dB versus 76 dB) to the participants. They found that participants were more likely to perceive the louder stimulus as longer than the standard stimuli ([Goldstone et al., 1978](#)). Similar results have also been found with sizes of squares ([Xuan et al., 2007](#); [Rammsayer and Verner, 2014](#)), flickering frequency ([Kanai et al., 2006](#)), and differences in the modalities ([Matthews et al., 2011](#); [Jones et al., 2009](#)).

Considering the well-known phrase, "time flies when you're having fun" recent studies on temporal perception have been focusing on the effect of emotion. Angrilli et al. examined the temporal distortion

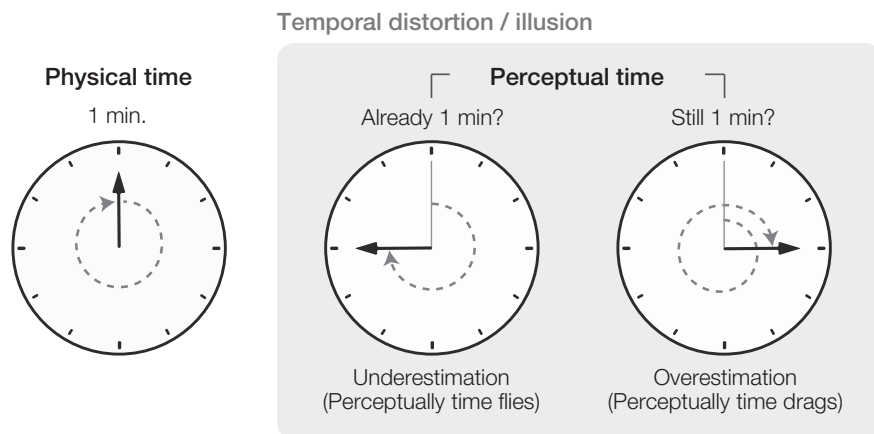


Fig. 2.1.1: The relationship between the temporal distortion effect and the internal clock

An abstract concept of the internal clock speed and the category of temporal distortion. When an observer overestimates time, this can be interpreted as the speed-up of the observer's internal clock, which gives the impression that the physical time in the rest of the world drags.

by a standardized and validated emotional visual material, the International Affective Picture System (IAPS: (Lang, 2005)) (Angrilli et al., 1997), suggesting that the duration of negative stimuli is judged longer than the duration of positive stimuli. This effect was also found in the auditory domain utilizing the International Affective Digitalized Sounds System (IADS: (Bradley and Lang, 1999)) (Noulhiane et al., 2007). Other researchers have tested this effect with emotional facial stimuli. Droit-Volet et al. reported a temporal overestimation for emotional faces compared with neutral faces (Droit-Volet et al., 2004). Specifically, the findings exhibited that the faces expressing anger were systematically judged to be of longer duration. The involvement of these arousal mechanisms in the effect of emotional stimuli can be explained by a few temporal perception models.

This relationship between arousal and the temporal distortion can be described in terms of the most conspicuous Internal-clock model (synonymous model: pacemaker-accumulator models) of time perception (Treisman, 1963; Gibbon et al., 1984). As mentioned below in section 2.4, a pacemaker of the internal clock releases a series of steady "time units" or "pulses" which are stored in the "accumulator." The number of the pulses then determines the perceptual time. However, in this model, the pacemaker fluctuates in speed by arousing inputs based on biological reactions such as the preparation of the body for action. Therefore, the arousing stimuli are thought to generate more pulses which are stored in the accumulator with the result that time is judged to be longer (Matthews and Meck, 2016). This model can explain why interesting moments are perceived to be shorter as opposed to boring moments. This is seen in the study by Wearden et al., which reported that participants judged the perceptual time passing to be

faster in relation to exciting videos (Wearden et al., 2014).

This pacemaker-accumulator model has therefore helped researchers interpret the effects of temporal distortions and how we perceive time without any specific receptor for the half-century since their introduction by Treisman (Treisman, 1963). Not merely the pacemaker-accumulator model, but many alternative models have been designed (*e.g.*, Walsh, 2003; Buetti and Walsh, 2009; Eagleman, 2008; Gibbon, 1977; Gibbon et al., 1984), predicated on different assumptions (see Section 2.4). Despite the ambiguity and diversity of time perception models, one particularly robust finding from the previous studies is that perceived duration seems to depend upon the magnitude (or arousal) induced by the stimuli, and apparent duration is usually a positive function of the intensity of the sensory signal.

2.2 Temporal experiment tasks

In this section, we introduce some key methods and experimental tasks to measure perceptual time and temporal distortion. In temporal perception studies, researchers often arbitrarily choose one temporal procedure from various methods due to empirical findings reporting a solid correlation between the results of different temporal tasks (Wearden and Lejeune, 2008; Gil and Droit-Volet, 2011). However, some studies suggest tasks involving temporal production are primarily dependent on the internal clock rate, whereas reproduction tasks depend on working memory capacity (Baudouin et al., 2006). Therefore, the selection of tasks used in the study should be performed with an in-depth examination of the differences in the cognitive processes.

Temporal perception studies are roughly classified into two main methods; prospective judgment and retrospective judgment (Matthews and Meck, 2016).

Prospective timing is the situation whereby the participant is aware of their feedback on temporal judgment as something that is important in a study and are prepared in advance. In contrast, in a retrospective judgment, the request for a temporal judgment comes unexpectedly after the stimulus presentation. As only one data per participant can be obtained by the retrospective judgment tasks, and the judgment by prospective judgment is thought to be influenced by the attentional and memory processes, most previous studies adopt tasks with prospective judgments.

Most studies of temporal perception, especially in the context of duration judgments, focus on the judgment of duration in range of a few hundred milliseconds to a few seconds. The subjective duration is generally assessed by combining the derived information from the temporal tasks with other psychophysical methods. For instance, after presentation of the two stimuli (to-be-timed in intervals and reference

intervals), the participant indicates which duration was longer (or shorter). The ratio of the response is then used to fit the psychophysical function, and the shift of the estimated function indicates distortion of time and gives the point of subjective equality (PSE).

Here we mention several major temporal perception tasks used in this study, from section 2.2.1- 2.2.3 which performs prospective judgment, followed by an example task situation when the target (to-be-timed) interval is 2,000 ms and the reference interval is 1,600 ms-2,400 ms in 200 ms step.

2.2.1 Bisection task (Church and Deluty, 1977)

The temporal bisection task was originally developed to test the predictions of the internal clock models developed by Church and Deluty. In this bisection task, first, the participants conduct the training phase in which they learn and store the duration of “Short” and “Long” reference durations. Usually, the reference stimuli in the training phase is a neutral condition stimulus, depending on what the to-be-timed target is (*e.g.*, Achromatic oval shape, Neutral evaluated emotion stimuli). Second, the test phase is where participants judge either the presented stimuli’s duration as “Short” or “Long” by retrieving the duration from the memory.

Training Memorize “Short” (1,600 ms) “Long” (2,400 ms)

2AFC Task Judge whether the target stimuli (probe duration 1,600 ms-2,400 ms in 200 ms step) is “Short” or “Long”

2.2.2 Duration discrimination task (Allan and Kristofferson, 1974)

Duration discrimination task (also known as the duration comparison task) is one of the tasks used from early history of temporal perception studies (Allan and Kristofferson, 1974). In this task, participants are instructed to judge the relative duration of two time intervals sequentially presented. The two presented stimuli consist of the reference stimuli and the comparison stimuli which is the to-be-timed target, generally counter-balanced across trials to avoid the serial-position effect.

Instruction To discriminate the longer stimuli presented.

2AFC Task Judge whether the longer interval was the reference stimuli (2,000 ms) or the comparison stimuli (probe duration 1,600 ms-2,400 ms in 200 ms step) presented either first or second.

2.2.3 Generalization task (Desiderato, 1964)

The generalization task shares a similar procedure as the bisection task; however the judgment is based on whether the duration of the stimuli is identical to the reference stimuli. The participants first conduct

the training phase to memorize a certain duration of the reference stimuli. Subsequently, in the test phase, participants judge either the presented duration of the to-be-timed target is the “Same” or “Different” by retrieving the duration from memory.

Training Memorize the reference duration (2,000 ms)

2AFC Task Judge whether the target stimulus (probe duration 1,600 ms-2,400 ms in 200 ms step) is “Same” or “Different” to the memorized reference duration

2.3 Evaluation of the perceived duration

As mentioned in the previous section 2.2, experimental tasks used to measure perceptual time and temporal distortion rely on relatively simple responses by the observer. However, researchers often employ psychophysical methods to extract the perceived duration of the interval and the level of discriminating intervals (temporal sensitivity,) by computing the point of subjective equality (PSE) and just noticeable difference (JND) from the psychometric function (Matthews and Meck, 2016). The psychometric function offers an advantage over simple measures, given that simple measures can be open to further interpretations in temporal perception studies (Meck, 1996).

2.3.1 Proportions of “long” responses

The response from major temporal perception tasks such as the bisection task (see section 2.2.1) and generalization task (section (Desiderato, 1964)) are analyzed by fitting a psychometric function to the proportion of “long” responses as a function of the reference durations. In this study, when the target interval is 2,000 ms and the reference interval is 1,600 ms-2,400 ms in 200 ms step, the probability of each reference interval (1,600, 1,800, 2,000, 2,200, 2,400 ms) judged longer is plotted (x -axis: reference stimulus duration, y -axis: the probability of “Longer” response). The probability and duration usually have a proportional relation since longer reference durations are easily judged to be longer, and vice-versa. The points are modeled by mathematical functions, typically a sigmoid function, such as the Weibull, logistic, or cumulative Gaussian distribution, which are collectively called the psychometric functions (Wichmann and Hill, 2001).

The fitted response usually takes an S-shape slope (see Figure 2.3.1 for an ideal psychometric function). A shift of the psychophysical function provides information about the effect of the independent variable (*e.g.*, color of the stimuli), and the slope of the function provides a measure of the variability of temporal representations (flatter = low sensitivity).

2.3.2 Point of subjective equality (PSE)

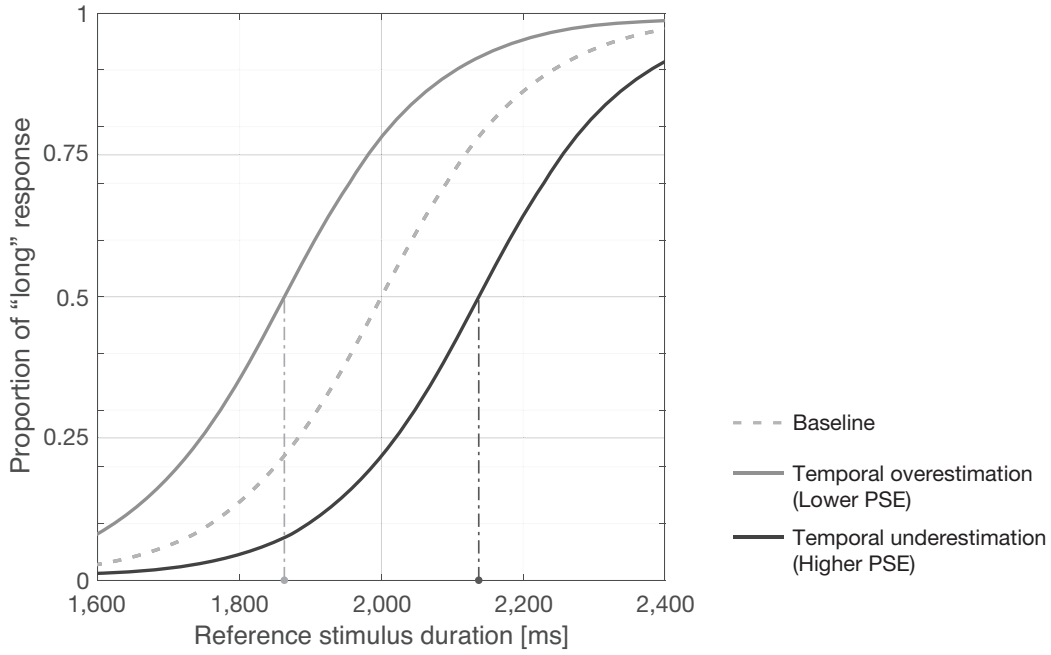


Fig. 2.3.1: An example psychometric functions with a different point of subjective equality (PSE)

The solid dark line represents a positively shifted psychometric function which indicates temporal underestimation. On the other hand, the solid gray line represents a temporal overestimated response. The PSE computed from the psychometric functions are exhibited as the black and gray dots on the x -axis.

Figure 2.3.1 exhibits an example of psychometric functions with different temporal perceptions. After a successful psychometric function fitting, the slope and intercept of the regression line are used to find the duration corresponding to the proportion of “long” responses of 0.5, which is called the PSE (Church and Deluty, 1977). In other words, the PSE indicates how long the reference stimulus must be to have the same apparent duration as the target (to-be-timed) duration. Therefore, lower PSE indicates an overestimation of temporal duration, and high PSE values are a sign of temporal underestimation.

$$\text{PSE} = \text{Duration} (p = 0.5) \quad (2.1)$$

Since the PSE can be easily computed from the intercept of the slope and proportion-of-long = 0.5, the PSE is defined as Equation 2.1, in which $\text{Duration} (p = x)$ is the duration for which the proportion of “long” response is x .

2.3.3 Just noticeable difference (JND)

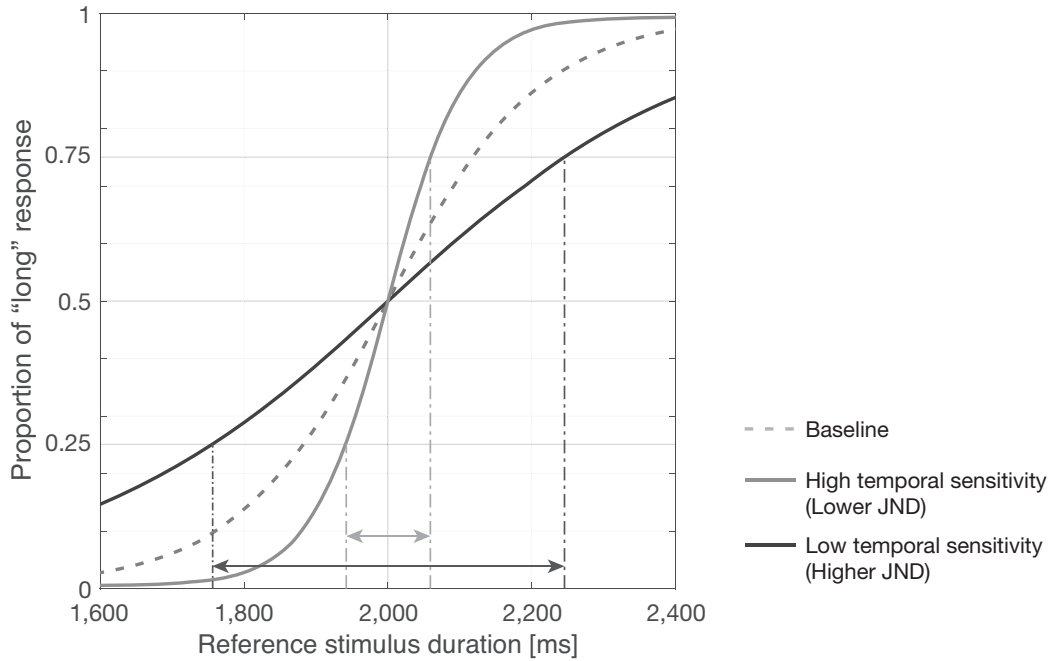


Fig. 2.3.2: An example psychometric functions with a different just noticeable difference (JND)

The solid dark and light lines represent a psychometric function under low and high JND responses, respectively. The horizontal dashed lines represent the duration corresponding to the proportion of “long” responses of 0.25 and 0.75, which is later used to compute the JND.

Figure 2.3.2 shows an example psychometric functions with different temporal sensitivity. As the name suggests, just noticeable difference (JND) is often loosely defined as the minimal physical difference that an observer can just notice. The JND is defined as Equation 2.2, in which $Duration(p = x)$ is the duration for which the proportion of “long” response is x . In other words, JND is half of the difference between the duration yielding a proportion-of-long = 0.25 and = 0.75 response in the psychometric function.

$$JND = \frac{Duration(p = 0.75) - Duration(p = 0.25)}{2} \quad (2.2)$$

A flat slope would result in a relatively larger JND reflecting temporal sensitivity, whereas a steep slope would imply a smaller JND and higher temporal sensitivity.

2.4 Theoretical accounts

Although there are many theories and computational modeling for temporal perception to explain the distortion effect of non-temporal factors, in this section we mention the two prominent models discussed in most previous studies and as models related to this thesis.

2.4.1 Internal-clock principal / pacemaker-accumulator model

The main idea of the internal-clock, which was to reach its fullest expression in the models of Treisman (Treisman, 1963), suggests that temporal judgment might be attributed to a biological source of temporal information. This abstract model contains the basic mechanism of the pacemaker-accumulator model, latterly proposed by Gibbon et al. (Gibbon et al., 1984). A schematic representation of the pacemaker-accumulator model is depicted in Figure 2.4.1.

As shown in Figure 2.4.1, the pacemaker-accumulator model consists of six main elements, namely: the pacemaker, switch, accumulator, working memory, reference memory, and the comparator. In this model, the pacemaker of the internal clock releases a series of “pulses” which flow into the accumulator after the switch closes. After the timing ends, the switch opens and stops the flow of the pulses. Both the pacemaker and the switching timing fluctuate in speed and timing by sustained attention to the stimulus. The adequate flow of pulses is thought to be modulated by the arousal, and the operation of the switch depends on how the stimulus attracts attention (Matthews and Meck, 2016). The number of pulses stored in the accumulator forms the representation of subjective duration which is transferred to the working memory and the long-term memory. In the pacemaker-accumulator model, temporal judgments are based on comparison of the working memory representation with the previously encoded pulse-counts in the long-term memory. Therefore, as the arousing stimuli can generate more pulses stored in the accumulator by the delay of the switch and/or increase of the pulse flow, the non-temporal factors may affect the perception of time.

2.4.2 Coding efficiency model

Recently, temporal perception models have also been developed through neuroscientific perspectives. Eagleman and Pariyadath proposed a model in which the subjective duration may be directly related to the total energy expended encoding the stimulus, such that the non-temporal factors which evoke larger neural responses entail a longer perceived duration. Furthermore, Eagleman and Pariyadath suggested that the temporal distortion effect by visual flickering stimuli saturates at approximately 8 Hz, which is

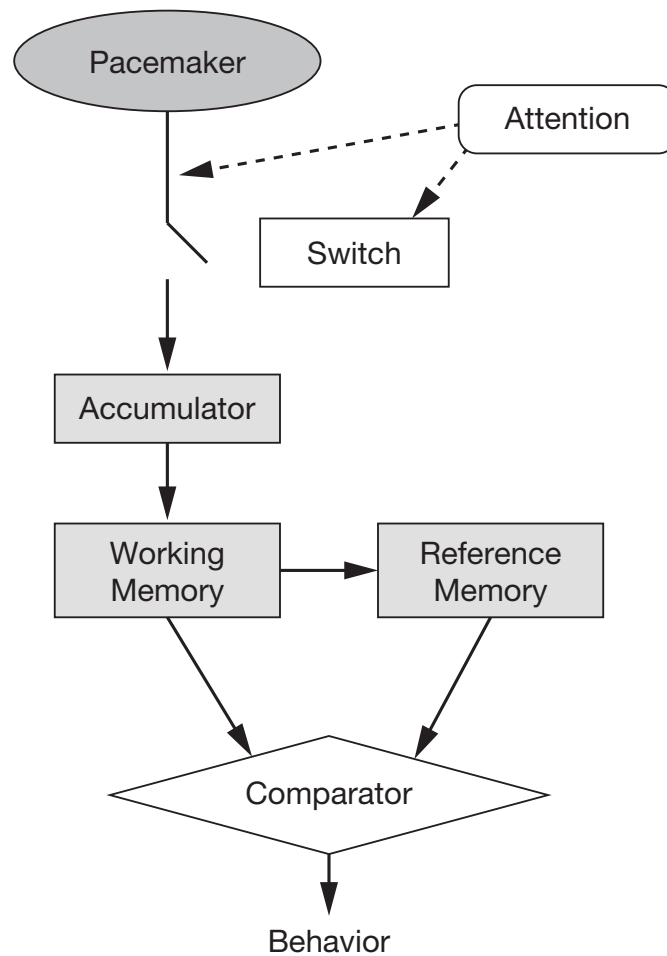


Fig. 2.4.1: A generic pacemaker-accumulator model (Adapted from [Matthews and Meck \(2016\)](#), modified after [Gibbon et al. \(1984\)](#))

In the pacemaker-accumulator model an accumulator counts the pulses generated by a pacemaker. The timing of the to-be-timed begins when the switch closes, allowing generated pulses to flow into an accumulator. The accumulated pulses in the accumulator form the representation of subjective duration. The amount can be modulated by both the change in pulse-ratio and the timing of the switch operation.

the similar saturation in the BOLD signal response to flicker in the V1 ([Eagleman and Pariyadath, 2009](#)).

To further confirm this effect, Noguchi and Kakigi conducted a magnetoencephalography study to elucidate how the brain converts sensory experiences into their time representations. In the study, a generalization task was conducted with asymmetric symbols that were displayed on the screen. As a result, the evoked response of the visual regions were larger for the stimuli that were classified as “long” as opposed to trials that were judged as “short” despite the identical physical durations and stimuli ([Noguchi and Kakigi, 2006](#)).

The temporal distortion caused by arousing the stimuli can also be described by this model. It is well known that the amygdala, clusters of nuclei located in the medial temporal lobe, are strongly related to emotion (LeDoux, 1998). Hence, a number of studies have exhibited that threatening stimuli such as angry facial expressions, activate the amygdala and the whole brain activity by intense stimuli, which may lead to temporal distortion.

2.5 Psychological studies on the functioning of Red/Blue

As color is indispensable to individuals' perceptual experiences of the world, its effect has been the subject of research since the early history of psychology. Studies show that colors surrounding us in our daily lives profoundly affect bodily functions, including mood and behavior (Babin et al., 2003; Kwaliek et al., 1988). The potential effect of color on our bodily functions has been extensively discussed after Hill and Barton reported that competitors wearing red clothing or body protection had a significantly higher chance of winning the 2004 Olympic Games in Athens (Hill and Barton, 2005). They explained that this is because the vividness of the red color increases the amount of testosterone they have in their bodies, which also correlates with their physical health, leading to a psychological advantage.

Although that study prompted much controversy, individuals have cognitive associations with specific colors. For instance, long-wavelength colors such as red are often considered dangerous and compelling, whereas short-wavelength colors like blue are perceived as relaxing. Furthermore, red explicitly captures individuals' attention and is associated with biological danger (Pomerleau et al., 2014; Buechner et al., 2014; Tchernikov and Fallah, 2010), whereas blue is often considered to evoke the opposite response. Numerous researchers have discussed the psychological effects of colors, with most studies explicitly focused on red and blue colors, as these are two of the three primary colors located at each end of the visible-light region. Assumptions on red-inducing arousal have also been extensively investigated through physiological measures such as electroencephalography (EEG) (Ali, 1972), galvanic skin response (Jacobs and Hustmyer Jr, 1974), and heart rate variability (Elliot et al., 2011).

In the EEG study, Ali presented red and blue lights directly on the eyes of the subject through a projector for 10 minutes. From the EEG recording during stimulation and following one minute resting condition, results showed a faster recovery of alpha waves by the blue lights compared to the red lights. As the alpha gain is strongly related to relaxation, Ali concluded greater cortical arousal following the presentation of the red light (Ali, 1972).

Jacobs and Hustmyer reported that after presenting the red, yellow, green, and blue screens for one

minute to subjects whose GSR, heart rate, and respiration was being recorded, red was significantly more arousing than the other colors with the increase of the skin conductance (Jacobs and Hustmyer Jr, 1974). Recently, HRV which is a non-invasive measure of the variation in time between each heartbeat, is also focused as a physiological indicator reflexing the autonomic nervous system (ANS) activity. Elliot et al. reported that participants' HRV decreased as a result of the presentation of red light, compared to blue or gray light, indicating a lower parasympathetic activity (Elliot et al., 2011).

As the effect of color emerges in physiological indices, color simply affects human behavior such as the cognitive performance. Some studies have reported that red enhances task performance compared to blue (Mehta and Zhu, 2009; Elliot and Aarts, 2011; Xia et al., 2016). Mehta and Zhu conducted several cognitive tests on 600 subjects to determine whether cognitive performance varied by color. Words or images were displayed against red, blue, or neutral backgrounds. As a result, red backgrounds enhanced the recall ability and attentiveness to detail-oriented tasks such as remembering words or checking spellings and punctuation. On the other hand, blue enhanced performance on creative tasks which required imagination (Mehta and Zhu, 2009). In contrast, some researchers suggest that the influence of red and blue on cognitive tasks is modulated by the difficulty of the task. Soldat et al. reported that when the difficulty of the test is high, the participants' accuracy was increased by blue letters than in the red. Conversely, when the test items were easier, the participants' accuracy in the blue and red had no significant difference (Soldat et al., 1997).

To obtain a unified explanation on these studies, Xia et al. conducted a study that combined the two factors (difficulty / type of task) to investigate the interaction on task performance. Xia et al. found that red enhanced the performance on a simple detail-oriented task. However, blue improved the performance on a difficult detail-oriented task as well as on both simple and difficult creative tasks, suggesting that the type of task and difficulty of the task together, modulate the effect of color on cognitive performances (Xia et al., 2016).

Altogether, the influences of color on cognition and behavior are seen as a result of learned associations, that is when different colors are accompanied by particular experiences and/or concepts (*e.g.*, red is often associated with danger: stop signs, warnings) (Elliot et al., 2007). Therefore, varied associations involving red and blue can induce alternative bodily functions; red induces arousal, while blue is relaxing.

2.6 Color to temporal perception

Unsurprisingly, the growing interest in colors' psychological effects on cognitive functions including the pursuit of their effect on temporal perception was no exception (see section 1.3). One of the early attempts to investigate the effect of color on temporal perception was reported in the 1960s. Since individuals' bodies have an intrinsic physiological reaction to color, which is reflected in psychological experience and functioning (Elliot et al., 2007), most studies focus specifically on the colors red and blue due to the saliency in wavelengths. Table 2.6.1 summarizes the methods and results of studies on the color red and blue.

Table 2.6.1 shows that relationships between color and temporal perception have been examined by various tasks in different durations; however existing research reports inconsistent findings. Smets et al. conducted a verbal estimation task and a reproduction task reporting an overestimation of blue light. However, while the luminance of lights was matched individually, the study failed to control for possible differences in the saturation of the different color stimuli (Smets, 1969). Caldwell and Jones also conducted a temporal estimation task, and the participants were instructed to estimate the passage of 30 s and 40 s in the presence of red, white, and blue lights, although results indicated that color did not exert consistent significant effects on color. Gorn et al. reported that temporal perception were shortened under blue light compared to red or yellow light, that is, warm colors was perceived longer than blue (Caldwell and Jones, 1985).

Unlike earlier investigations using a tachistoscope, recent studies use displays for stimulus presentation, enabling control of the stimuli's physical properties, such as brightness and saturation. Gorn et al. reported that temporal perception was shorter with a blue background than with red or yellow backgrounds; warm colors were perceived for a longer time than blue (Gorn et al., 2004). Shibasaki et al. reported that the perceived duration of red stimuli were perceived longer than that of blue stimuli. However, those results differed between the sexes; only men overestimated the duration of the red stimuli (Shibasaki and Masataka, 2014). Shibasaki et al. concluded that this is due to the arousal effect of color red which consists principally longer wavelengths (Walters et al., 1982; Jacobs and Hustmyer Jr, 1974). However, contrary to this study, Thönes et al. reported a temporal overestimation in blue stimuli compared to red (Thönes et al., 2018). In studies of temporal perception, especially in the context of duration judgments, arousal and the perceptual magnitude of the perceiver, represents an important driving factor. Therefore, it is necessary to carefully match the two colors' physical properties in light of the stimuli intensity and arousal. As these studies indicate, the potential effects of color on temporal perception are still not

Table 2.6.1: Summaries of studies on red/blue on time perception (Reproduced and modified after Kinzuka et al. (2022) under CC BY 4.0)

Study	Method		Results (Judged longer)	Statistical values
	Task	Interval Duration		
Smets (1969)	Estimation	45 s	Blue > Red	$t = 1.55$, Cohen's $d = 3.07^\dagger$
Caldwell and Jones (1985)	Production	30 s, 40 s	No effect	—
Gorn et al. (2004)	Estimation	17.5 s	Blue < yellow/Red	Blue-Yellow: $F(1, 47) = 3.95$ Blue-Red: $F(1, 59) = 5.21$ Blue: $t = 1.05$, Cohen's $d = 0.35^\dagger$ Red: $t = 1.00$, Cohen's $d = 0.33^\dagger$
Katsuura et al. (2007)	Production	90 s, 180 s	Blue > Red	$F(1, 72) = 14.42$, $\eta_p^2 = 0.17$
Shibasaki and Masataka (2014)	Comparison	0.4 s \sim 1.6 s	Blue < Red ¹	$t = 2.917$, Cohen's $d = 0.81$
Thönes et al. (2018)	Comparison	1.6 s \sim 2.4 s	Blue > Red	$t = 1.478$
Yang et al. (2018)	Comparison	0.75 s \sim 1.35 s	ipRGC activation: High > Low	

[†] Recalculated using reported values¹ Only for male participants

consistent. These inconsistent results on the effect of color may be attributed to the lack of control over the physical properties. However, focusing on these inconsistent results may assist in clarifying the temporal perception mechanism.

2.7 Brightness to temporal perception

Given the large growth of research in both the research field of human vision and temporal perception, it was a natural consequence that researchers would begin to have an interest on the effect of luminance on temporal perception space with the color effect.

As luminance is one of the conspicuous magnitude dimensions in visual sensation, luminosity is one of the most focused non-temporal stimuli attributable to a general principle that subjective duration is positively related to the stimuli magnitude. The early scientific inquiry of the effect of stimulus luminance on perceived duration was conducted by Goldstone et al. In a series of studies, Goldstone et al. used a red light-emitting diode (LED) in a duration comparison task and asked the participants to judge which of the two durations (comparison or standard) was longer. The comparison stimulus was judged to be longer when the luminance was more intense as opposed to when it was standard, indicating that higher illumination increased subjective temporal perception (Goldstone and Goldfarb, 1964; Goldstone et al., 1978). Several subsequent studies have replicated the luminance effect in temporal judgment tasks using a tachistoscope (Brigner, 1986; Long and Beaton, 1980).

More recently, Xuan et al. investigated whether judgments of duration are modulated by the magnitude information in various dimensions, such as space, quantity, and time. In a Stroop-like interference paradigm, participants judged whether the duration of the two continuous stimuli was longer. The results indicated that the temporal accuracy was higher when luminance intensity and the to-be-measured duration were congruent in different temporal tasks, in other words, when the short-presented stimulus was dim and the longer stimulus bright (Xuan et al., 2007). Similar to other non-temporal aspects of temporal illusions, the prominent relationship between luminosity and subjective temporal perception is also reported to be affected by the relative, perceptual representations of luminance (Casini and Macar, 1997). Notably, absolute and relative stimulus brightness both predominantly affect temporal perception. Matthews and Stewart conducted several experiments fluctuating both target and background stimuli luminance. Surprisingly, the effect of the stimulus magnitude on the temporal perception depends upon the background: against a high-intensity background, dim stimuli were judged to be of longer durations, so were bright stimuli on dark backgrounds (Matthews et al., 2011). These recent studies raise the possibility

that the perceptual representation of luminance magnitude, which modulates temporal perception, may also depend on the interplay between external stimuli intensity and cognitive internal processing.

2.8 Pupillary light reflex

The pupillary light response (or pupil/pupillary light response/reflex: PLR) is a sharp constriction of the pupil in response to light to reduce the amount of light that falls into one eye reaching the retina. The size of the pupil can change drastically under certain circumstances, from its maximum (8 mm in humans) to its minimum (2 mm in humans) (Mathôt, 2020). Historically, the PLR was considered as a purely reflexive response for physical adjustment of the light flux; however, recent studies have shown that the PLR is not merely a reflex but includes many cognitive effects due to inputs from cortical innervation (Mathôt, 2018). In fact, the pupil starts to constrict with a latency of 200 ms-250 ms, following exposure to light (Ellis, 1981) and reaches its peak constriction after roughly 1,000 ms-2,000 ms (Mathôt, 2020). In most other studies, cognitive influences on the PLR are not directly contrasted with direct exposure to brightness or darkness. However, empirically, cognitive influences on the PLR are generally small compared to the light-induced constriction. (Pupil diameter change of less than 1% to approximately 5% (Mathôt et al., 2013).)

The PLR is driven by all known types of photoreceptors, such as rods, cones, and intrinsically photosensitive retinal ganglion cells (ipRGC/mRGC) on the retina (Markwell et al., 2010; Ostrin, 2018). The latency of the ipRGCs response is much slower to light input than rods and cones. Therefore ipRGCs start responding and keep the pupil constricted for as long as the light is on (Gamlin and Clarke, 1995; Gamlin et al., 2007). In other words, with light stimulation, initial pupil constriction is primarily attributed to rod and cone photoreceptors, following light offset attributed to the ipRGCs.

Because the pupil diameter is under the control of the autonomic nervous system (ANS), PLR also shares a similar pathway. The pupil constrictor and dilator muscles receive antagonistic impulses separately from the parasympathetic and sympathetic autonomic nervous systems. Crucial neuronal control of the PLR is illustrated in Figure 2.8.1 (Chougule et al., 2019).

As shown in Figure 2.8.1, the photoreceptors on the retina, including the ipRGCs stimulate the SCN which is connected to the sympathetic LC, and OPN which is connected to the parasympathetic EWN. The EWN supplies the parasympathetic pre-ganglionic nucleus that innervates the iris sphincter muscle and the ciliary muscle; EWN is therefore the major cholinergic center for pupillary constriction. Additionally, light has an inhibitory effect on the sympathetic activity in the PVN through the SCN attenuated by

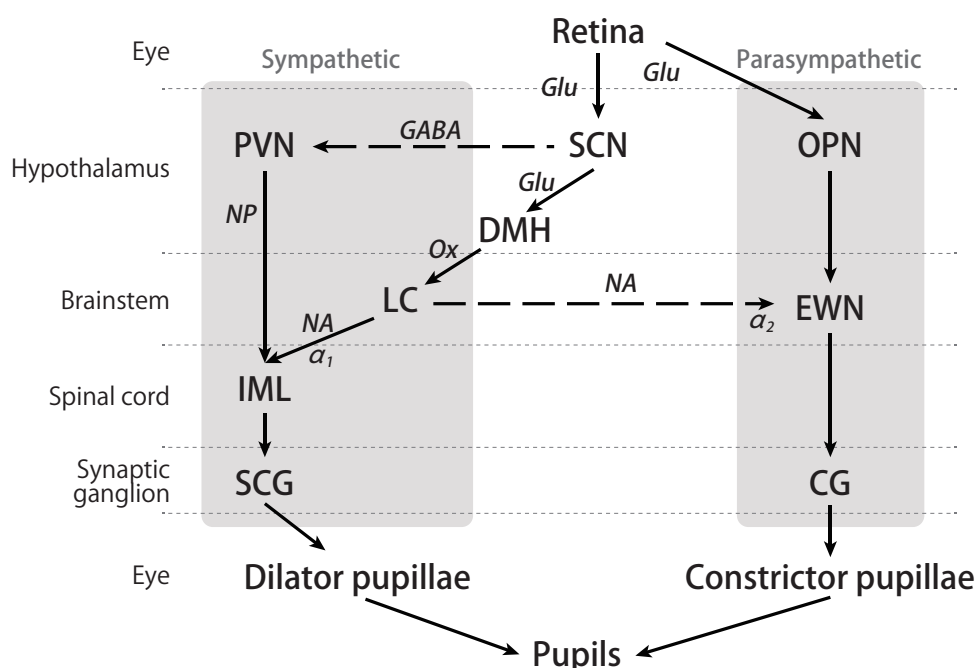


Fig. 2.8.1: Neuronal control of the PLR (Reproduced and modified from Chougule et al. (2019) under CC BY 4.0)

Neural connections

Solid lines: excitatory connections

Dashed: inhibitory connections

Regions and Nucleus cells

SCN: SupraChiasmatic Nucleus

DMH: DorsoMedial Hypothalamus

LC: Locus Coeruleus

CG: Ciliary Ganglion

SCG: Superior Cervical Ganglia

PVN: ParaVentricular Nucleus

OPN: Olivary Pretectal Nucleus

EWN: Edinger Westphal Nucleus

IML: Intermedio-Lateral spinal cord

Neurotransmitters

Glu: Glutamate

VP: Vasopressin

Ach: Acetylcholine

GABA: γ -amino-butyric acid

Ox: Orexin

NA: NorAdrenaline/NorEpinephrine

Adrenoceptors

α_1 : excitatory adrenoceptors

α_2 : inhibitory adrenoceptors

sympathoexcitation (represented by the top-left dashed line in Figure 2.8.1). The sympathetic efferent system including the LC and SCN, regulate the baseline pupil size by the dilator muscles. The LC is especially active when an organism is aroused, awake, and alert; and has a wide projection to the IML of the spinal cord. Since the LC is the central source of noradrenaline/norepinephrine in the brain, the pupil diameter is known to act as a proxy for the physiological arousal state (Bradley et al., 2008; Einhäuser et al., 2008). Among them, the neural activity of norepinephrine-containing neurons in the brainstem nucleus, the LC is often interpreted as the driving factor for the pupil diameter (Aston-Jones and Cohen,

2005; [Murphy et al., 2014](#)). Specifically, the increased activity in the LC and the belonging sympathetic nerve system are strongly associated with pupil dilation ([Kang et al., 2014](#); [Aston-Jones and Cohen, 2005](#)).

Mentioned previously, although the constriction and dilation pathways are roughly distinct, pupil diameter depends on the interplay between antagonistic parasympathetic and sympathetic activities. The LC inhibits the EWN; that is, LC activity causes pupil dilation not only by activating the sympathetic nerve system but also by inhibiting the parasympathetic nervous system at the EWN (represented as the middle dashed line in Figure 2.8.1). Therefore, the LC is considered the most influential mediator of the PLR ([Peinkhofer et al., 2019](#)).

2.9 Pupil and temporal perception

Temporal perception has also been recently studied by the neuromodulation of the pupil diameter ([Faber, 2017](#)). [Suzuki et al.](#) sought to establish a link between the norepinephrine (NE/NA) system and duration judgment ([Suzuki et al., 2016](#)). In the study, monkeys (Japanese macaques) were trained to perform a temporal production task with an oculomotor response. The monkeys were required to generate a memory-guided saccade to the cue location after memorizing the mandatory delay duration following the cue onset. Through the task, pupillary response was continuously recorded since the pupil diameter is closely linked to the internal factors and neuromodulatory signaling. [Suzuki et al.](#) reported that the saccade latency on the production task and the size of the pupil diameter were negatively correlated. Specifically, as the shorter saccade latency can be explained by an overestimation of time, pupil dilation may be related to subjective time expansion (perceived longer).

Interestingly, a recent study by [Kruijne et al.](#) adopted the EEG and pupil size recording to a temporal perception study as a measure of the magnitude of the sensory response ([Kruijne et al., 2021](#)). In this study, observers conducted a temporal discrimination task where two flashing stimuli demarcated the start and end of a to-be-timed duration. These visual stimuli could be either in the same or a different location on the screen, specified in advance per trial. This was to induce different sensory responses due to neural repetition suppression; and diminished neural activation that results from repeated stimulus presentation ([Henson, 2003](#)) without changing the arousal states. Their results suggested that the intervals with changing locations were perceived to have longer durations than those presented in the same location, that is, duration perception was affected by the neural response magnitude and repetition suppression, despite the control of arousal or surprise. Although the pupillary recording was intended for indices of

the sensory response's magnitude, and their focused time window of the pupillary response was after (and not during) the to-be-timed interval, this is one of the few studies that imply the connection between temporal perception and pupillary response.

In addition, a more recent study by Warda et al. sought to investigate the relationship between the pupil size and the perceived duration in the sub-second and supra-second range. In this study, Warda et al. evaluated two different hypothesis. First, to replicate the result of the primate studies conducted by Suzuki et al., in human participants (Suzuki et al., 2016; Suzuki and Tanaka, 2017); and second to test the pupil size indexes error processing in temporal perception, suggested by Toscano-Zapién et al. (2016) rather than perceived duration per se. From the results of temporal bisection tasks in the sub-second and supra-second time domain, pupil diameter was larger during stimulus processing when shorter intervals were overestimated but also during and after stimulus offset when longer intervals were underestimated. These results suggest that pupil diameter can track errors in interval timing, especially in processing sub-second intervals.

Most importantly, the connection between high-level cognition and the pupil is now the center of pupillometry research. This is because the pupil size can reflect various cognitive aspects as a window to neural substrates of cognition (*e.g.*, Laeng et al., 2012; Mathôt, 2018; Joshi and Gold, 2020). Coincidence or destiny, well known non-temporal factors that cause temporal illusions (*e.g.*, emotion, color, luminance, surprise, attention, cognitive load), seem to strongly relate to the size of the pupil.

3

Hypothesis Testing: The effect of Red/Blue on temporal perception and pupillary response induced by different equiluminant conditions

A similar version of this chapter has been published as:

Yuya Kinzuka, Fumiaki Sato, Tetsuto Minami, & Shigeki Nakauchi. “The effect of red/blue color stimuli on temporal perception under different pupillary responses induced by different equiluminant methods.” *Plos one*, 17(6), e0270110. 2022.

Figures reproduced under [journal policies](#) and [CC BY 4.0](#).

3.1 Red longer? or blue longer?

The effect of color has been the subject of research since the early history of psychology due to its ubiquitousness. Studies show that colors surrounding us in our daily lives profoundly affect bodily functions, including mood and behavior (Babin et al., 2003; Kwallek et al., 1988). The potential effect of color on our bodily functions has been extensively discussed after Hill and Barton reported that competitors wearing red clothing or body protection had a significantly higher chance of winning the 2004 Olympic Games in Athens (Hill and Barton, 2005). They explained that this is because the vividness of the red color increases the amount of testosterone they have in their bodies, which also correlates with

physical health, leading to a psychological advantage. Although that study prompted much controversy, people have cognitive associations with specific colors. For instance, long-wavelength colors such as red are often considered dangerous and compelling, whereas short-wavelength colors such as blue are perceived as relaxing. Furthermore, red explicitly captures our attention and is associated with biological danger (Pomerleau et al., 2014; Buechner et al., 2014), whereas blue is often considered to evoke the opposite response. Moreover, since color emerges in physiological indices, it is known to affect human behavior, such as cognitive performance (Mehta and Zhu, 2009; Xia et al., 2016) (see section 2.5 for more on psychological studies on the functioning of red/blue).

Unsurprisingly, the growing interest in colors' psychological effects on cognitive functions includes the pursuit of their effect on temporal perception was no exception. In 2011, a BBC science documentary show, *Horizon, 2011-2012, Do You See What I See?* explored the perception of color through a number of psychology and neuroscience experiments. In this hour-long program, neuroscientist Beau Lotto conducted a study on 150 people to see if the color changes our perception of time. Participants entered a red and blue-lighted room and were asked to give a sign when they think a minute has passed. Interestingly, the people who bathed in red light perceived that a minute lasts an average of 11 seconds longer than those standing in the blue room. This result indicates that color can speed up time, and people tend to overestimate the time by red (Robinson, 2011). Even though this study might lack of scientific basis, the show served as an opportunity to tell the general public that color can modulate temporal perception.

We also know from experience that perceptual time is not isomorphic to physical time, and our subjective experience of the passage of time is significantly influenced by non-temporal aspects, such as emotions, experiences, and our internal states. Psychophysical and behavioral techniques help demonstrate how non-temporal cognitive information modulates the subjective perception of time to reveal the underlying mechanism of temporal perception. Many studies have been conducted using stimuli with different visual sensory inputs to investigate how the apparent duration of a specific time interval is influenced by lower-order characteristics and by color. Since the 1960s, the potential effects of red and blue on temporal perception have been studied to determine the fundamental mechanism. Table 2.6.1 (Reproduced and modified after Kinzuka et al. (2022)) summarizes the methods and results of several temporal perception studies concerning color.

Table 2.6.1 shows the relationship between color and temporal perception examined using various tasks of different durations; however, existing research displayed inconsistent findings. Smets et al. reported an overestimation of blue light in a verbal estimation and reproduction task. While the luminance of the lights

was individually matched, the study did not account for potential changes in the saturation of different color stimuli (Smets, 1969). Caldwell and Jones also conducted a temporal estimation task wherein participants estimated the passage of 30 s and 40 s in the presence of red, white, and blue lights. However, the results indicated that color had no consistent significant effects on temporal estimation (Caldwell and Jones, 1985)

The abovementioned studies show an inconsistency in the potential effects of color on temporal perception and indicate a lack of clarity regarding the probable mechanism of temporal perception modulation. Arousal is known to play an essential role in the distortion of perceived time, as suggested by the conspicuous internal-clock model (synonymous with the pacemaker-accumulator model) (Matthews and Meck, 2016; Treisman, 1963; Gibbon et al., 1984). Indeed, studies that suggest that red stimuli can cause temporal overestimation, generally explain the mechanism by increased arousal. According to such models, arousal induced by the color red accelerates the internal clock (more time passes on the internal clock than in real life) or the speed of the pulse emitted per unit time (more pulses are stored in the accumulator), resulting in an overestimation of the duration of the red stimuli. Consequently, because the arousal induced by colors may primarily cause temporal modulation via its hue, the inconsistent results could be attributed to the challenge of controlling physical properties such as hue and luminance. In fact, physically brighter stimuli tend to be perceived longer (*e.g.*, Goldstone et al., 1978; Casini and Macar, 1997), and a recent study showed that perceptual brightness, which induces different pupillary responses, is sufficient to elongate the subjective time (Kinzuka et al., 2021). Hence, focusing on these inconsistencies may help us better understand the mechanism of temporal perception. The physical properties of the two colors, especially luminance and saturation, must be carefully matched and compared, as other physical aspects of color can affect individual arousal and subjective magnitude.

To overcome these limitations, we conducted a two-interval duration-discrimination task to assess the effect of equiluminant colors on temporal perception. Specifically, we colorimetrically controlled the saturation of the presented red/blue stimuli and matched the luminance with subjective equiluminant to segregate the former's effect on temporal perception (Experiment 1: Section 3.2). Additionally, since short-wavelength light (blue) is more effective than long-wavelength light (red) in evoking a pupillary light reflex (PLR) even at identical physical luminance (*e.g.*, Szabadi, 2012; Herbst et al., 2011; Janisse, 1977), the second study evaluated the temporal distortion effect using pupil diameter-based equiluminant stimuli (Experiment 2: Section 3.3). In fact, some recent studies have suggested an interesting connection between pupillary response and subjective passage of time (*e.g.*, Suzuki et al., 2016; Kruijne et al., 2021) (see section 2.9); however, few studies have focused on the effect of the PLR (Kinzuka et al., 2021), which

can be largely modulated by the physical properties of the stimuli to be timed. Therefore, with this study, we aimed to clarify the effect of color on temporal perception with controlled physical properties and to investigate the relationship between pupillary response, notably PLR and temporal perception.

3.2 Subjectively equiluminant condition (Experiment 1)

3.2.1 Introduction

In the first experiment, the red/blue stimuli were colorimetrically controlled in saturation, and the luminance was matched based on subjective equiluminance. This experiment mainly focuses on **Research question 1**, aforementioned in section 1.4.

3.2.2 Materials and methods

Participants

All experimental procedures and methods were in accordance with the ethical principles outlined in the Declaration of Helsinki and approved by the Committee for Human Research at the Toyohashi University of Technology, and the experiment was strictly conducted in accordance with the approved guidelines of the committee. Informed written consent was obtained from participants after procedural details had been explained. The experiment involved 26 students (22 men, 4 women; age range: 21-27 years; $M = 22.34$, $S.D. = 1.44$) at the Toyohashi University of Technology. Eye movement data from two participants were excluded from pupillary analyses because the number of artifacts detected in the trials exceeded the 60% threshold, which could not be interpolated in the preprocessing phase. In the behavioral data analysis, trials with a reaction time (RT) > 10 s were also removed from the analysis, assuming poor task performance. This criterion rejected only 0.18% of the trials. None of the participants reported color vision deficiency; all had normal or corrected-to-normal vision.

Stimuli and apparatus

The experiment was conducted in a dimly lit room. MATLAB 2016a (The MathWorks, Natick, MA, USA) and the MATLAB toolbox, Psychtoolbox 3 (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007), were used for stimulus presentation. The instructions and stimuli were presented on a liquid-crystal display (LCD) monitor (Display++, Cambridge Research Systems Ltd, Rochester, UK) with a resolution of $1,920 \times 1,080$ pixels and a refresh rate of 120 Hz. An eye-tracker (EyeLink 1000 Plus, SR Research, Oakland, Canada) was installed below the presentation display, centered on participants. The participant's head was fixed on a chin rest at a viewing distance of 70 cm from the display. All behavioral responses were

provided using a trackball or a numeric keypad with unnecessary keys removed.

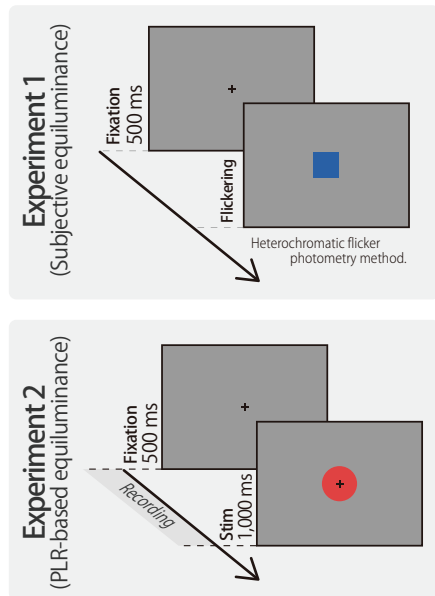
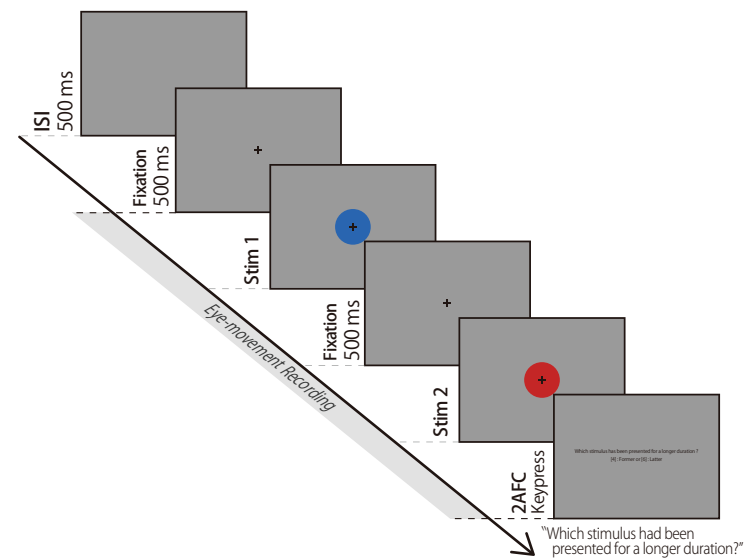
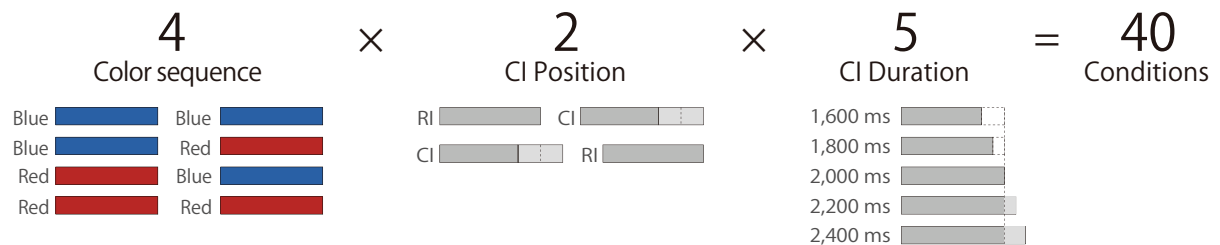
In the temporal discrimination task (main task), we used two-color disk stimuli with a 10 deg visual angle diameter. We individually adjusted the luminance of the red stimulus in the adjustment task to match the subjective luminance of the blue stimuli, and saturation was controlled despite the difference in hues. In the adjustment task, we used a square stimulus (4 deg \times 4 deg visual angle) instead. In both tasks, we displayed all experimental stimuli at the center of the screen. The xy coordinates of the blue stimulus and the initial coordinates of red in the CIE1931 color space were (0.2286, 0.1936) and (0.4899, 0.3362), respectively. The background luminance remained constant at 37.83 cd/m² for achromatic luminance ($x, y = 0.3127, 0.329$). During the stimulus presentation, the fixation cross was located at the center of the screen for pupil diameter recording.

Procedure

The experiment was divided into two tasks: an adjustment task and a duration-discrimination task. The adjustment task consisted of eight trials based on the heterochromatic flicker photometry method (Bone and Landrum, 2004; Wagner and Boynton, 1972). The procedure of the duration-discrimination task was based on recent temporal perception studies (Thönes et al., 2018; Kinzuka et al., 2021), with 320 trials conducted over four sessions. Figure 3.2.1 shows the protocol for one trial in each session and all the experimental conditions.

Each trial in the adjustment task (Figure 3.2.1A, left panel) began with the presentation of a fixation cross at the screen center, followed by a flickering stimulus consisting of red and blue squares at the same location. The adjustments were made based on heterochromatic flicker photometry, a method for determining subjective equiluminance for a pair of heterochromatic stimuli in temporal alternation (Bone and Landrum, 2004). The flickering frequency of the two colors was set to 10 Hz, following previous studies (Pokorny et al., 1989). The participants were instructed to adjust the intensity of the red stimulus until the flickering was mostly reduced (modulate to the null flickering point). Specifically, participants rotated the trackball upward or downward to increase or decrease the luminance of red (the Y-value), respectively, and pressed the button to select the displayed luminance. The initial Y-value of red was randomized over the eight trials, and the overall mean luminance was used in the duration-discrimination task.

Subsequently, the participants performed the two-interval duration-discrimination task (Figure 3.2.1A, right panel). Two-color stimuli were presented continuously on the screen, followed by a 500 ms inter-

A**Luminance adjustment task****Duration discrimination task****B****Fig. 3.2.1:** Experimental protocol for one trial (Exp.1 & Exp.2)

(A) Depiction of one trial sequence in the experiment. Stim1 and Stim2 in the duration-discrimination task refer to either the reference interval (RI) or comparison interval (CI). In Experiment 2, the luminance of the color stimuli was adjusted based on PLR amplitude instead of subjective equiluminance. (b) Illustration of experimental conditions for the duration-discrimination task.

stimulus interval (ISI). The red stimuli were individually generated by the Y-value determined in the adjustment task. The fixation point was displayed continuously while eye movement was recorded. In a single trial, one stimulus was presented for 2,000 ms (reference interval; RI), while the duration of the other stimulus varied between 1,600 ms and 2,400 ms in five steps (comparison interval; CI), separated by a 500 ms interval. Following continuous presentation, the participant indicated which visual stimulus was presented for a longer duration using the numeric keypad. The “4” key was used for the former stimulus, while “6” was used for the latter. No feedback was provided. The order of CI/RI positions was randomized and counterbalanced across sessions following a within-subjects design; the three factors were fully cross (color sequence, CI position, and CI duration). Each of the 4 (color sequence) \times 2 (CI position) \times 5 (CI duration) = 40 combinations were presented for 8 times, resulting in a total of 320 trials per participant (Figure 3.2.1B).

The eye tracker was adjusted before the first and the subsequent sessions, as necessary, using a standard five-point calibration. Participants were neither instructed to nor discouraged in performing temporal-judgment strategies, such as counting up and other rhythmic activities known to increase temporal sensitivity (Grondin et al., 2004).

Data analysis

An eye tracker (EyeLink 1000 Plus, SR Research, Oakland, Canada) recorded binocular pupillary responses at a sampling rate of 500 Hz. We did not instruct the participants when to blink during eye movement measurements since we placed importance on the temporal task; hence, we interpolated blinks before the main analysis using cubic-spline interpolation (Mathôt et al., 2013) in MATLAB 2018b. Pupil size was expressed in arbitrary diameter units (EyeLink values), which were generated by the eye tracker. In the time-course analysis, pupil diameter data were baseline-corrected by subtracting the mean pupil size during -50 ms to 0 ms (stimulus onset) and filtered using a 20-point moving average.

The participants reported which stimulus had a longer perceived duration, either RI (fixed duration of 2,000 ms) or CI (1,600 ms-2,400 ms in 200 ms steps), in the two-interval duration-discrimination task. To estimate the psychometric functions, the participants’ responses (proportion of CI stimuli judged longer) were modeled by fitting the logistic psychometric function using the Palamedes toolbox in MATLAB (Prins and Kingdom, 2018) and computing the point of subjective equality (PSE) and just-noticeable difference (JND) (see section 2.3). The “threshold” and “slope” parameters used in the toolbox function were left at their default free parameters for all color sequence conditions (B-B, B-R, R-B, and R-R; “B” and “R” for blue and red, respectively, representing the CI-RI combination). Since

the PSE represented the level of duration continuum which is subjectively identical to the duration of the RI, the PSE was used to compare the effect of hue on temporal perception. The statistical analyses were performed using R for macOS version 3.5.1 and a repeated-measures analysis of variance (ANOVA) function, *anovakun* (version 4.8.2). Pairwise comparisons of the main effects were corrected for multiple comparisons using Shaffer's Modified Sequentially Rejective Bonferroni (MSRB) (Seaman et al., 1991) procedure. In the ANOVA, the partial η (η_p^2) was reported as a measure of association strength (effect size). In addition to the analysis in R, JASP (JASP Team, 2020) was used to compute the Bayes factor BF_{10} in a Bayesian repeated-measures ANOVA, and BF_{01} as relative evidence to interpret the effect of the null hypothesis.

3.2.3 Results

Adjustment task

In the adjustment task, the participants conducted a luminance-matching task based on heterochromatic flicker photometry to determine subjectively equiluminant Y-value for the red stimulus. Figure 3.2.2 shows the distribution of the adjusted (subjectively equiluminant) Y-values.

The mean average of the adjusted Y-value was 0.308, almost identical to the Y-value of blue (0.300). Therefore, we conducted a one-sample Bayesian *t*-test with a test value of 0.300 on the adjusted Y-values to statistically support this hypothesis. The analysis indicated a Bayes factor $BF_{10} = 0.427$ and $BF_{01} = 2.34$, which can be interpreted as anecdotal evidence to support H_0 over H_1 (Ortega and Navarrete, 2017). The mean average of the adjusted Y-value is statistically identical.

Duration judgment

In the duration-discrimination task, the participants indicated whether the RI (duration fixed at 2,000 ms) or CI (variable duration: 1,600 ms-2,400 ms in steps of 200 ms) stimulus was perceived to have a longer duration. The order of the presented CI was not predetermined, and the CI was presented first (CI position: CI-RI) or second (RI-CI) with equal probability. Each CI-longer probability was used for psychometric function fitting for each duration step of the CI to compute the PSE and JND. The mean psychometric function shown in Figure 3.2.3 was derived by fitting a psychometric function to the average of the five duration steps of the CI. The difference in duration was computed by subtracting the RI duration from the CI duration.

Each solid line in Figure 3.2.3 represents a fitted psychometric function. The color conditions of the

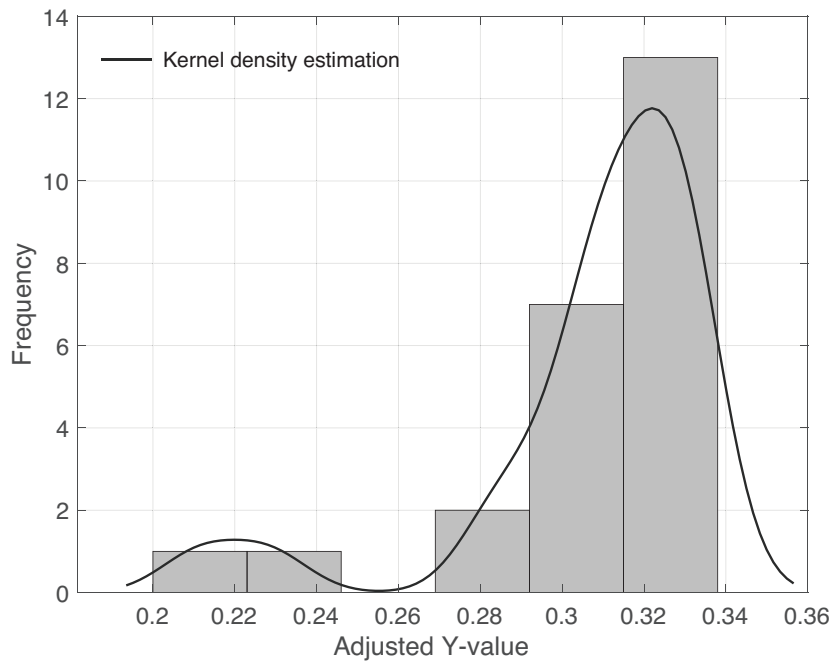


Fig. 3.2.2: Histogram and distribution fit of the adjusted Y-values

Gray histogram represents the heterochromatic flicker photometry adjusted Y-value distribution.

The solid black line shows the estimated density by the kernel smoothing function.

RI and CI stimuli are indicated via the labels (*e.g.*, R-B represents the RI stimulus being red and the CI stimulus being blue). The dashed vertical lines represent the PSEs under each condition, proportional to the 50% probability of the function; the PSE denotes a specific duration of the CI judged equivalent to the RI, which is presented for 2,000 ms. A relative shift in the fitted function was observed in the incongruent stimulus comparison, whereas no shift emerged in the congruent stimulus comparison. Figure 3.2.4 shows the PSE determined using a psychometric function.

A one-way repeated-measures ANOVA was performed on the color sequence, the main effect of which was significant ($F[3, 69] = 6.5613, p = .0006, \eta_p^2 = 0.2060$) in the PSE; therefore, a post-hoc *t*-test was also conducted. The post-hoc analysis showed that the two incongruent color sequences, R-B and B-R, differed significantly, as the PSEs were smaller when the CI color was red rather than blue ($t[23] = 3.4053, \text{adjusted } p = .0146$), whereas no other color sequence combination showed significant differences. Additionally, the Bayesian repeated-measures ANOVA indicated $BF_{10} = 36.5$ and $BF_{10} = 1.027$ for PSE and JND, respectively. The PSE shift suggests a temporal overestimation of red stimuli compared with blue stimuli. Contrary to the PSE, the effect of color sequence on JND did not reach statistical significance ($F[3, 69] = 2.7088, p = .0518, \eta_p^2 = 0.1054$), suggesting that temporal sensitivity

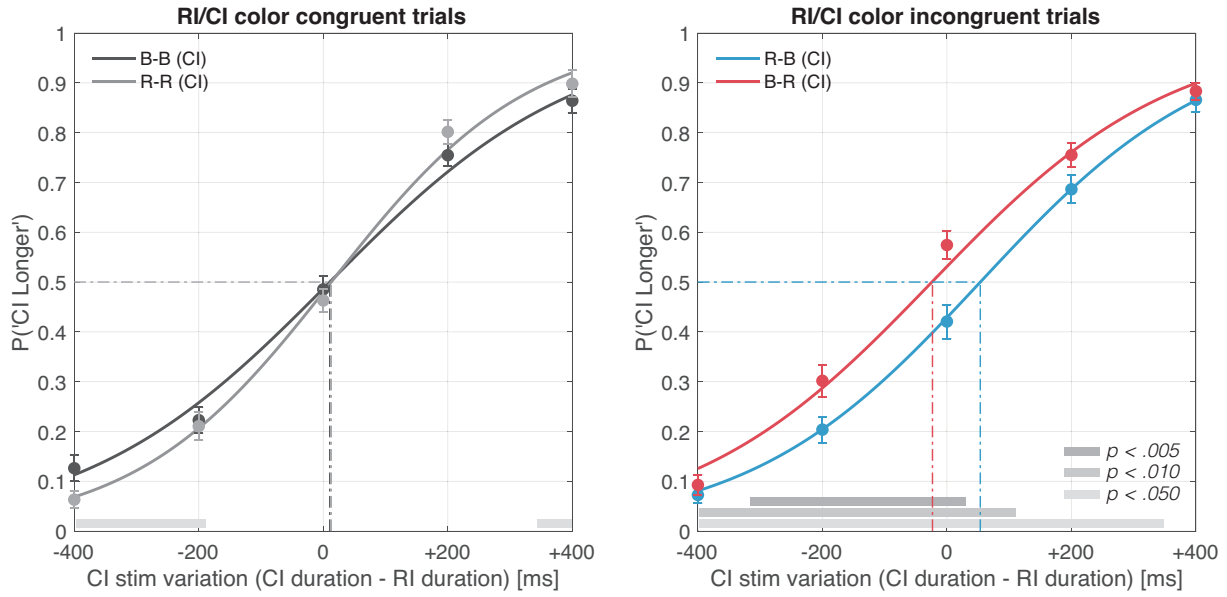


Fig. 3.2.3: Mean psychometric functions (subjective equiluminance)

Left panel: Psychometric function fitting by the proportion of comparison interval-longer (CI) response in congruent color sequence. Right: For an incongruent color sequence. Abbreviations: B-blue, R-red, CI-comparison interval, RI-reference interval.

did not differ by color sequence.

Pupillary response

All pupillary responses to the red and blue stimuli in RI and CI durations were averaged across conditions after the raw pupil data were preprocessed, as explained in the Methods section. Figure 3.2.5A shows the grand average of pupil responses during a -50 ms to $1,600$ ms stimulus onset under both color stimuli and presentation (RI or CI) conditions. The range was set to the shortest CI duration and the responses were aligned according to the presentation onset.

As shown in Figure 3.2.5A, a typical PLR was observed for each color stimulus. Thus, the peak PLR amplitude was computed using the average minimum pupil diameter between the 300 ms- $1,300$ ms time domains, as depicted in Figure 3.2.5B. This figure shows that the two-way repeated-measures ANOVA (color condition \times stimuli-type condition) on the effect of peak PLR amplitude revealed a significant main effect of color condition ($F[1, 23] = 31.7220, p < .001, \eta_p^2 = 0.5797$). Post-hoc comparisons also suggested a significant difference between the color conditions in each stimulus-type condition. However, the stimulus-type condition, did not reach statistical significance ($F[1, 23] = 0.0059, p = .9393, \eta_p^2 = 0.0003$). These results suggest that blue evoked a larger PLR than red, despite the two colors being

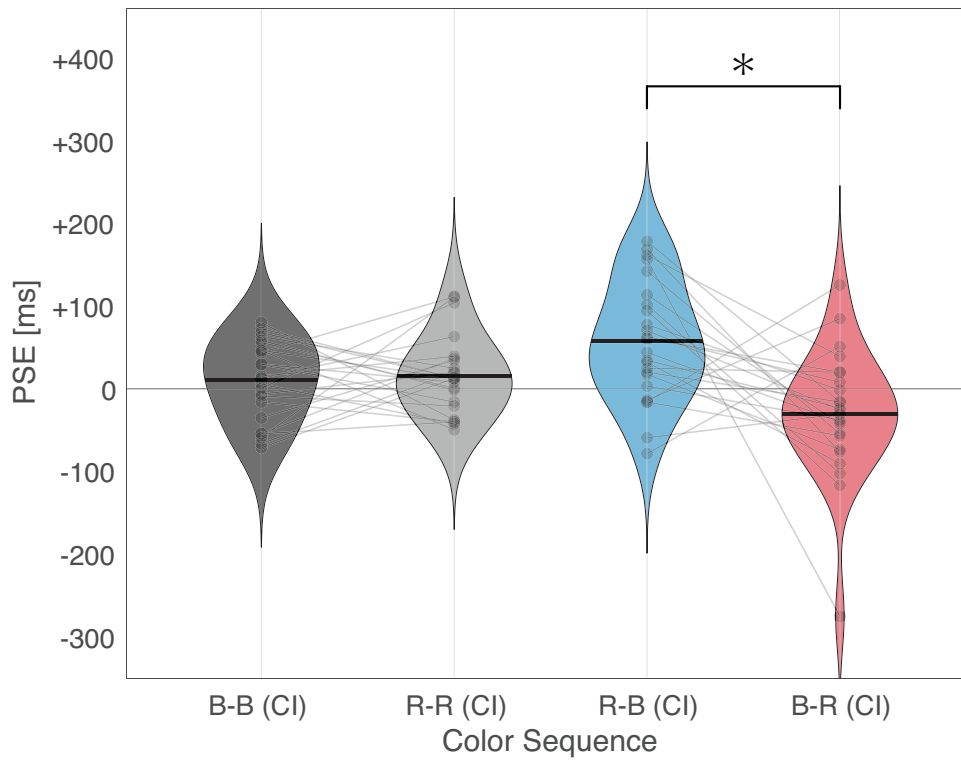


Fig. 3.2.4: Mean PSE of each color sequence

Violin plots of mean PSE as a function of stimulus sequence. The plots show the data distribution with a solid black line for the mean of the data. The overlaid semi-transparent dot indicates the mean value for each participant's data. * Indicates statistically significant ($p < .05$) differences in the analysis of variance and post-hoc testing. Abbreviations: B-blue, R-red, CI-comparison interval, PSE-point of subjective equality.

individually matched based on subjective equiluminance.

3.2.4 Discussion

In the first study, we investigated whether the perceived duration of a visual stimulus was affected by hue in subjective equiluminant conditions. This was also conducted to examine previous studies' results that contradict each other (*e.g.*, Shibasaki and Masataka, 2014; Thönes et al., 2018; Yang et al., 2018), under stringent control of physical properties, since these may be due to lack of control of the physical properties, especially the luminance of red and blue stimuli. Furthermore, we performed pupillometry to investigate the relationship between the PLR response and temporal perception, as a recent study suggested possible associations between the two (Kinzuka et al., 2021), with the former differing under stimuli of different wavelengths (Szabadi, 2012). Based on the known effects of arousal on temporal perception and the vital function of red, we hypothesized that the participants would overestimate (perceive longer) the duration

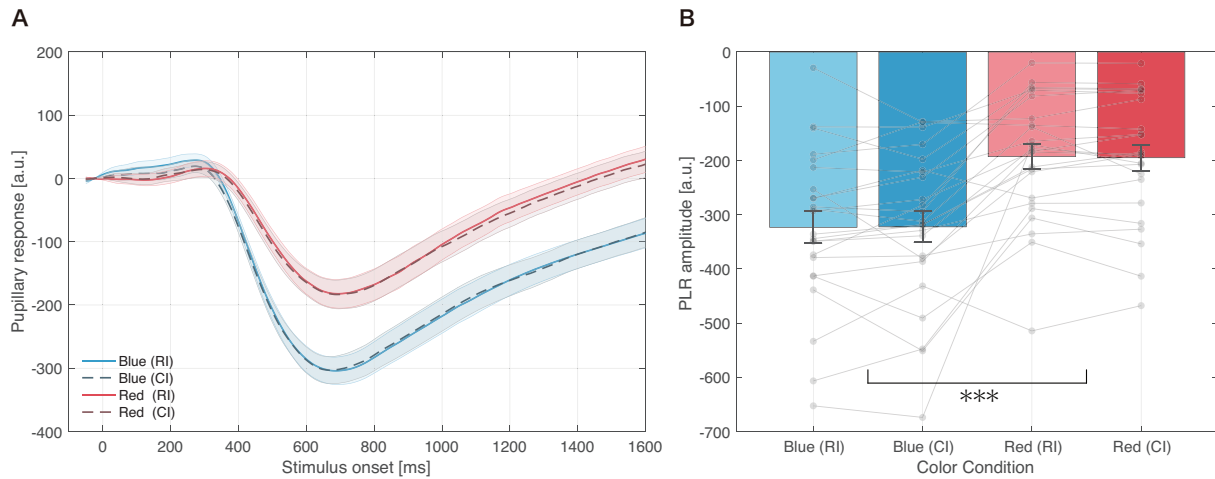


Fig. 3.2.5: Pupillary response to each color stimulus (subjective equiluminance)

(A) Mean change in pupil diameter from stimulus onset. Each line represents pupillary responses to RI and CI stimuli, whereas the shaded regions are standard errors of the mean. The x -axis range is limited to 1,600 ms, the shortest CI duration. **(b)** Mean peak PLR amplitude of each color condition. Peak PLR amplitude is determined as the minimum pupil diameter between 300 ms-1,300 ms in the time domain. *** Indicates a statistically significant ($p < .001$) main effect by ANOVA. The semi-transparent dots indicate each participant's data. Abbreviations: ANOVA-analysis of variance, CI-comparison interval, PLR-pupillary light reflex, RI-reference interval.

of red relative to blue.

The participants performed a two-interval duration-discrimination task at supra-second range intervals. According to the psychometric function analysis, the shift in the fitted function indicated that the duration of red stimuli was perceived as longer than that of blue stimuli (Figure 3.2.3, right panel). The mean difference in the PSE suggested that the durations of the blue and red stimuli were perceived as identical when the red stimulus was actually displayed 88 ms shorter (4.28%) than the blue stimulus (Figure 3.2.4).

These behavioral results replicated those of previous studies (*e.g.*, Gorn et al., 2004; Shibasaki and Masataka, 2014; Smets, 1969) that found that observing emotional expressions involving the color red can lead to temporal distortion by increasing the perceivers' arousal levels (Angrilli et al., 1997; Noulhiane et al., 2007)

Moreover, we must emphasize that this effect was observed even when the colors of the two stimuli were controlled for saturation (colorimetric adjustments in terms of the CIE1931 color space) and luminance differences (individually adjusted to subjective equiluminance using the heterochromatic

flicker photometry method). Our results suggest that the temporal distortion effect of red and blue is primarily driven by hue and that the effects of luminance and saturation are partially limited. Moreover, notwithstanding the adoption of the heterochromatic flicker photometry method to satisfy subjective equiluminance conditions, the mean average of the adjusted Y-value was almost identical, and the red and blue stimuli were also closely physically equiluminant in mean.

Furthermore, when we examined the pupillary responses, the PLR profile differed considerably, especially in amplitude. At the PLR peak for the blue stimulus, the pupil diameter was 1.66 times larger than that for the red stimulus (Figure 3.2.5). Since the PLR is driven by known photoreceptors, such as rods, cones, and intrinsically photosensitive retinal ganglion cells (ipRGCs) (Markwell et al., 2010), all of which have different sensitivity characteristics (Mathôt, 2018), the amplitude of the PLR to red/blue stimuli is known to differ (Wardhani et al., 2022). Szabadi et al. reported that short-wavelength light is more effective than isoluminant long-wavelength light in evoking the PLR because of the stimulation of melanopsin-containing photoreceptors (Szabadi, 2012). Our pupillary response data also showed that the PLR amplitude differed according to hue under subjective equilibration.

Bombeke et al. reported that differences in pupil diameter could modulate the magnitude of the initial feedforward response in the primary visual cortex and could, therefore, represent a confounding variable in studies investigating the neural influence of psychological factors (Bombeke et al., 2016). Suzuki et al. also discovered that stimuli that induce larger constrictions causally reduce the amount of light emitted to the retina, causing a drop in EEG signals, specifically steady-state visual evoked potentials (SSVEPs; an EEG that reflects the attention level to visual stimuli, typically recorded from occipital channels) recorded via electrodes located in the occipital area (Suzuki et al., 2019a). Since the apparent duration is typically known as a positive function of sensory signal intensity, various factors leading to a larger PLR in response to blue stimuli may explain the effect of color on temporal perception based on sensory signals. In conclusion, our findings suggest that red stimuli were temporally overestimated compared to blue stimuli under subjective (nearly physical) equiluminance. However, as the PLR differs according to the hue of the stimulus, its effect on temporal perception must be clarified to fully elucidate the potential effect of color among inconsistent research findings. Hence, to determine the relationship between temporal perception, hue, and pupillary responses, we conducted an additional control study with equiluminant stimuli based on PLR-matched luminance.

3.3 PLR-matched condition (Experiment 2)

3.3.1 Introduction

The findings in Experiment 1 suggest that red stimuli were temporally overestimated compared to blue stimuli under subjective (nearly physical) equiluminance. However, the PLR amplitude differed according to the hue of the stimulus. Therefore, in this experiment, the luminance of the red/blue stimuli was controlled through pupil diameter-based equiluminance. This experiment mainly focuses on the explication of **Research question 1** and **Research question 3** (see section 1.4).

3.3.2 Materials and methods

Participants

As with Experiment 1, all experimental procedures and methods were in accordance with the ethical principles outlined in the Declaration of Helsinki and approved by the Committee for Human Research at the Toyohashi University of Technology. Informed written consent was obtained after all procedural details were explained. Sixteen students (11 men, 5 women; age range: 20-34 years; $M = 25.69$, $S.D. = 3.65$) at the University of Oslo took part in the experiment. Two participants' eye movement data were excluded from pupil analyses, and 2% of the trials were rejected based on excessive reaction time. The rejection criteria for both eye movement data and behavioral data were identical to those in Experiment 1.

Stimuli and apparatus

The task was conducted in a different dimly lit room using MATLAB 2019a (The MathWorks, Natick, MA, USA) and MATLAB's Psychtoolbox, as mentioned in Experiment 1. The experimental stimuli were presented on an LCD monitor (P2213, Dell Inc.) with a resolution of $1,680 \times 1,050$ pixels and a refresh rate of 60 Hz. Colorimetric calibrations were conducted in advance for linear light output, and maximum luminance was corrected to 120 cd/m^2 to match the display specifications in Experiment 1. The apparatus arrangements also followed those in Experiment 1, except that the viewing distance was set to 66 cm from the screen. All behavioral responses were delivered via a numeric keypad with unnecessary keys removed.

The chromatic properties of the stimuli presented in the temporal discrimination task (main task) were identical to those in Experiment 1. However, the luminance of the stimuli was computed individually in the PLR-matching task. In this task, the luminance of the colored disks (diameter of 10 deg visual angle) varied at $Y = 0.22, 0.25, 0.28, 0.31$, and 0.34 .

Procedure

The procedure of the temporal discrimination task was nearly identical to that in Experiment 1. However, instead of the heterochromatic flicker photometry method, a PLR-based method was used in Experiment 2 (Figure 3.2.1A, left panel). In the PLR-matching task, each trial began with a presentation of the fixation cross for 500 ms followed by a red/blue disk for 1000ms at the center of the screen. The participants were instructed to view the stimuli passively. The two factors were fully crossed ($2 [\text{color}] \times 5 [\text{luminance}] = 10$ combinations) and randomly presented in a total of 50 trials per participant over two sessions. After stimulus presentation, the pupillary response was analyzed offline to determine a specific Y-value of blue. After preprocessing the pupillary data, the average PLR peak of all ten conditions was computed, and a linear regression analysis was performed to fit the discrete data points of luminance and PLR amplitude for both red and blue. Finally, luminance was evaluated via a fitted polynomial at the point where the PLR amplitude of red became equivalent. Simply put, the Y-value of blue that matched the PLR amplitude of red ($Y = 0.300$) was calculated. This calculated value was used to generate the blue stimulus in the following duration-discrimination task.

Followed by a sufficient break, the participants performed the two-interval duration-discrimination task (Figure 3.2.1A, right panel). As mentioned above, the procedure of the main task was identical to that of Experiment 1. Figure 3.2.1B depicts the combination of the 40 experimental conditions.

Data analysis

All aspects of behavioral data analysis were analogous to those in Experiment 1, whereas pupil size and eye movements were measured using the SensoMotoric-Instruments RED500 (SMI, Berlin, Germany) eye-tracking system at a sampling rate of 250 Hz. A nine-point calibration was performed before each session in the PLR-matching and duration-discrimination tasks. In both phases, participants were not instructed when to blink, and, thus, blinks and artifacts were interpolated before analysis using the same method as in Experiment 1 (Mathôt et al., 2013). Trials that retained additional artifacts, computed by thresholding peak changes in the velocity of the pupillary response, were excluded from analysis.

Pupil size was measured in SI units (mm) by the eye tracker. Because of the specifications of the eye-tracking system, the units varied from those in Experiment 1. Measurements in terms of absolute units may not be entirely invariant to factors such as viewing distance and are, thus, somewhat arbitrary (Mathôt et al., 2018). Therefore, for all time-course analyses conducted in this study we used baseline-corrected relative values, which consider random fluctuations in pupil size over time and allowed us to compare

results in different units. As for Experiment 1, pupil diameter data were filtered using a 20-point moving average.

3.3.3 Results

PLR-matching task

Raw pupil data were preprocessed, as explained in the methods section (Section 3.3.2). Figure 3.3.1A shows the pupillary response for one participant.

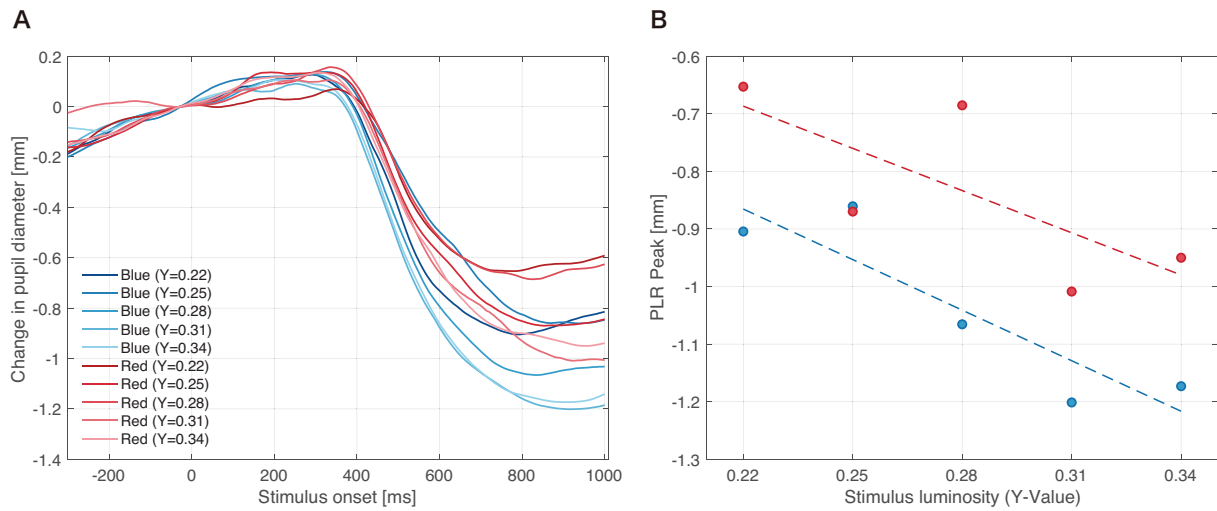


Fig. 3.3.1: Example pupillary response and peak PLR amplitude

(A) One participant's mean pupillary response to different hues and luminances (color and luminance: two (color) \times five (luminance) = ten combinations). Solid lines represent pupillary responses for each condition. **(b)** An example of mean peak PLR amplitude for each color condition. PLR diameter is computed as the minimum pupil diameter. The two dashed lines represent the fitted linear regression model, composed of discrete luminance and peak PLR amplitude data points, for red and blue stimuli, respectively. Abbreviations: PLR-pupillary light response.

The typical PLR profile was observed from the responses in hue and luminance conditions; that is, a tendency for (1) PLR amplitude (constriction amount) to increase with luminance and (2) blue to induce a prominent PLR. The first finding can be explained by pupil constriction in response to brightness, a function of retinal illuminance control of physical inputs from the ambient environment (Mathôt, 2018). Second, as short-wavelength light is more effective than long-wavelength in evoking the PLR, pupil constriction was larger for the blue stimuli. Therefore, we computed the average of the minimum pupil

diameter between the 400 ms-1,000 ms time domains in each condition, as shown in Figure 3.3.1B, with discrete data points of luminance and PLR peaks. Although Watson and Yellott reported a unified formula wherein luminance and pupil diameter had a logarithmic relationship over a wide range of luminances (10^{-4} to 10^4 cd/m²) (Watson and Yellott, 2012), the intensity of the stimuli used in this study was limited to a modestly narrow luminance range (*e.g.*, approximately 26.4-39.6 cd/m² in achromatic luminance). Hence, we concluded that linear regression provided adequate fitting accuracy, as indicated by the dashed lines in Figure 3.3.1B.

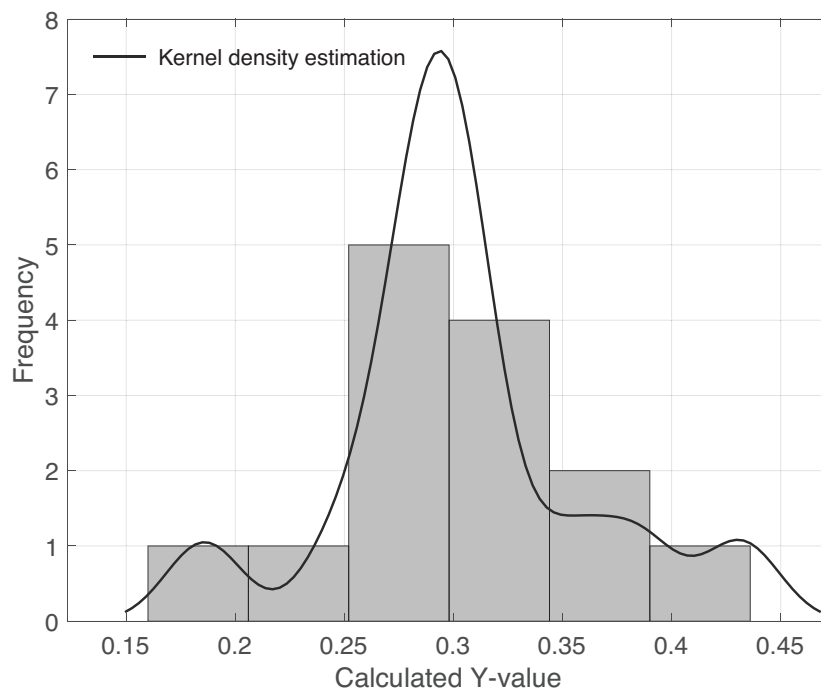


Fig. 3.3.2: Histogram and distribution fit of the calculated Y-values

Gray histogram represents the calculated Y-value distribution. The solid black line shows the estimated density by the kernel smoothing function.

Figure 3.3.2 shows the distribution of the calculated Y-values based on the linear regression results. The mean calculated Y-value was 0.3037 (*S.D.* = 0.0586).

Pupillary response

As previously conducted, we tracked pupil diameter changes induced by the presentation of color stimuli in CI positions and all CI durations. Figure 3.3.3A shows the grand average of the pupil response between

50 ms before and 1,600 ms after stimulus presentation under each color and stimulus-type condition. Furthermore, the profile of a typical orienting response (approximately 200 ms from onset) (Wang and Munoz, 2015) and the PLR were observed (approximately 300ms-700 ms from onset). Figure 3.3.3B shows the minimum mean pupil diameter of the PLR, computed by the average of the minimum peak PLR diameter between the 300ms-1,300 ms time domains.

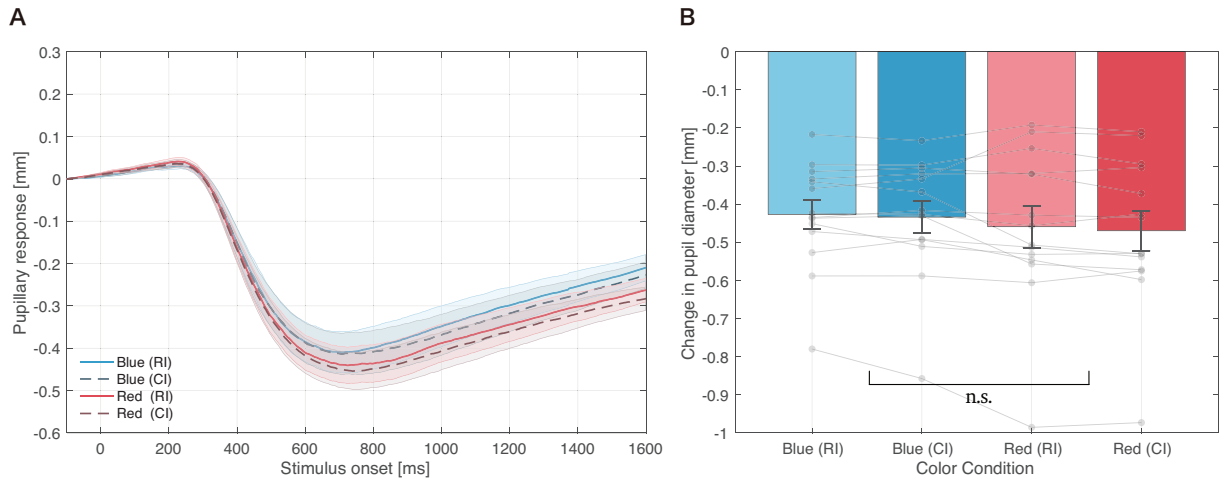


Fig. 3.3.3: Pupillary response to each color stimulus (PLR-based equiluminance)

(A) Mean change in pupil diameter from stimulus onset. Each line represents pupillary responses to RI and CI stimuli, whereas the shaded regions are standard mean errors. (b) Mean peak PLR amplitudes for each color condition. Peak PLR amplitude is determined as the minimum pupil diameter between 300 ms-1,300 ms in the time domain. The overlaid semi-transparent dots indicate each participant's data. Abbreviations: CI-comparison interval, PLR-pupillary light reflex, RI-reference interval.

Two-way repeated-measures ANOVA (color condition \times stimulus-type condition) on the effect of peak PLR amplitude showed no significant main effect on color condition ($F[1, 13] = 2.5119, p = .1370, \eta_p^2 = 0.1619$) or stimulus-type condition ($F[1, 13] = 2.9737, p = .1083, \eta_p^2 = 0.1862$). These statistical findings support the fact that PLR matching was performed.

Duration judgment

The CI-longer probabilities for all CI durations were again used for psychometric function fitting. The PSEs for each color sequence condition (B-B, R-R, R-B, and B-R) were calculated by fitting a cumulative normal function and determining the 50% point. Figure 3.3.4 shows the mean psychometric function

computed using the average of all participants' CI-longer proportions in each CI duration condition.

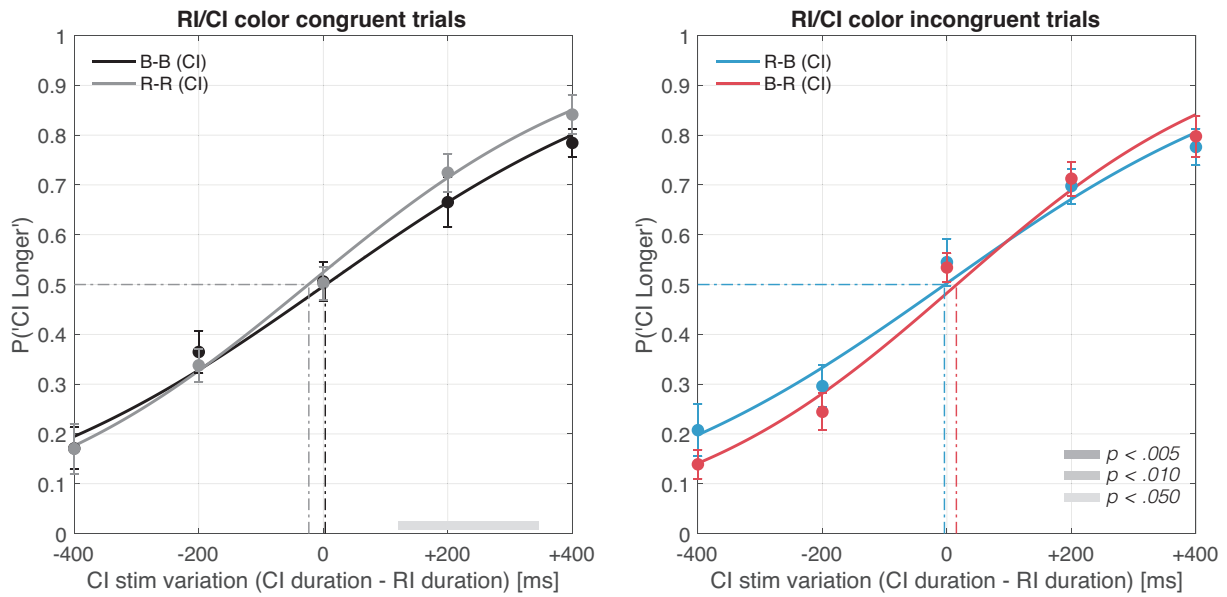


Fig. 3.3.4: Mean psychometric functions (PLR-based equiluminance)

Left panel: Psychometric function fitting according to the proportion of comparison interval-longer (CI) responses in congruent color sequence. Right: For incongruent color sequence. Abbreviations: B-blue, R-red, CI-comparison interval, RI-reference interval.

From the estimated psychometric function, no significant shift was observed in congruent- or incongruent stimulus comparisons. The computed PSEs and JND were used for statistical testing. A one-way repeated-measures ANOVA was conducted on each color sequence; the effect for the PSE was not significant ($F[3, 39] = 1.1105, p = .3565, \eta_p^2 = 0.0616$), and the effect size was relatively small (Tabachnick and Fidell, 2007). In contrast, a significant main effect was confirmed for the JND ($F[3, 39] = 3.1195, p = .0369, \eta_p^2 = 0.1935$); however, none of the pairs in the post-hoc comparisons reached statistical significance. Bayesian repeated-measures ANOVA indicated $BF_{10} = 3.012$ and $BF_{10} = 1.718$ for the PSE and JND, respectively. The Bayes factor of the JND analysis ($BF_{10} = 1.718, BF_{01} = 0.582$) reaching statistical significance in the classical ANOVA, indicated anecdotal evidence to support H1 over H0 (Ortega and Navarrete, 2017; Dienes, 2014). Notably, the statistics suggested no shift in the PSE-in other words, no significant temporal distortion due to the colors.

3.3.4 Discussion

To clarify the causal role of PLR amplitude induced by the to-be-timed stimuli and temporal perception, we replicated the first experiment in the second control experiment, excluding the equiluminant method, to investigate whether the perceived duration of the visual stimulus is affected by hue in PLR-matched conditions. This objective was based on two study backgrounds: (1) previous studies investigating the temporal distortion effect on hue show inconsistent results, which may be due to the failure of stimulus intensity matching; and (2) pupil diameter differs depending on the hue, which can play a role in temporal distortions, in addition to the arousal level induced by the hue. To the best of our knowledge, this study is the first attempt to investigate the relationship between the PLR response, temporal perception, and stimulus color.

Regarding PLR matching, Figure 3.3.3 illustrates that the PLR profile and peak constriction were similar among the hue conditions. As PLR amplitude generally differs in equiluminant color conditions because of stimulation of different photoreceptors, the results suggest adequate individual PLR matching in the first task. Specifically, the mean Y-value applied for the blue stimuli was 0.284, smaller than that for red (0.300). Since blue light is more effective in evoking the PLR (Szabadi, 2012), the actual value is expected to be lower than the computed value.

Statistical analysis suggested no significant temporal distortion via the hue condition, even though arousing stimuli are typically reported to be perceived longer. Many researchers have reported that observing emotional expressions can cause temporal distortion by increasing perceivers' arousal levels (*e.g.*, Noulhiane et al., 2007). Moreover, because red is considered a color of arousal, it can induce time overestimation. However, interestingly, the mean luminance to match the PLR amplitude was smaller for blue than for red, in this study. By comparing the physical luminance of the stimuli in Experiment 1, blue was adjusted to be darker in this study, whereas red was almost identical (Y-values of 0.300 and 0.284, respectively). Considering that "apparent duration is typically a positive function of the sensory signal intensity," red should have been perceived even longer, as the luminance of the comparative blue was adjusted to be smaller. In conclusion, our findings suggest that the temporal distortion effect of hue does not occur under PLR-based equiluminance, and it may be plausible that stimulus intensity, especially the physical luminance and arousal, is not the sole driving factor of temporal distortion.

3.4 Discussion

This study investigated whether the color of a visual stimulus affects its perceived duration in different equiluminant conditions to uniformly explain inconsistent research findings (see Table 2.6.1 for the results of previous temporal perception studies).

In Experiment 1, the red/blue stimuli were matched by subjective luminance using heterochromatic flicker photometry. From the behavioral results, a shift in the PSE was observed in incongruent color conditions, indicating an overestimation of red stimuli compared to blue stimuli. In contrast, our analysis suggests no JND modulation in temporal judgments. These behavioral results aligned with those of previous studies (*e.g.*, Smets, 1969; Gorn et al., 2004; Shibasaki and Masataka, 2014) that observing emotional expressions involving the color red can lead to temporal distortion. Hence, the overestimation of the duration of red stimuli in Experiment 1 may be due to the hue-induced arousal effect. Notably, this effect was observed even when the colors of the two stimuli were controlled for saturation (colorimetric adjustments in the CIE1931 color space) and subjective luminance; consequently, the adjusted luminance was also physically equiluminant. However, continuous pupillary recordings revealed significant differences in the PLR between the two stimuli. The blue stimulus induced notable constriction relative to the red stimulus. Several researchers have reported the possibility of differences in pupil diameter to directly modulate the magnitude of the response in the primary visual cortex, and stimuli that induce larger constrictions can causally reduce the amount of light entering the retina, leading to a drop in EEG amplitude in the primary visual cortex (Bombeke et al., 2016; Suzuki et al., 2019a).

Moreover, because apparent duration is typically a positive function of sensory signal intensity, pupillary responses such as the PLR should also be considered alongside physical aspects as factors that modulates the subjective passage of time. Therefore, we conducted a control experiment that adapted the duration-discrimination task to PLR-based equiluminant conditions (Experiment 2). Psychometric functional analysis in Experiment 2 revealed no significant distortion of duration according to hue, when the PLR was individually matched; the overestimation of the duration of the red stimulus faded when the stimulus luminance was matched based on the PLR amplitude.

An additional two-way repeated-measures ANOVA on the effect of the PSE, with color sequence as a within-subjects factor and experiment condition as a between-subjects factor, was conducted to support the notion that the PSE effect significantly differs when the PLR is not controlled (Experiment 1) vs. when it is controlled (Experiment 2). Note that these analyses were conducted on data with unequal sample sizes due to different participant numbers in the experiments. ANOVA results and descriptive results of

the PSE are shown in Table 3.4.2 and Table 3.4.1, respectively. The analysis revealed a significant main effect on experimental condition ($F[1, 36] = 6.205, p = .017, \eta_p^2 = 0.147$), and on the interaction of color sequence and experimental condition ($F[3, 108] = 4.807, p = .004, \eta_p^2 = 0.118$). Therefore, simple main effects analysis was performed to reveal the degree to which experiment condition is differentially effective at each color (Table 3.4.3), and vice-versa (Table 3.4.4). In addition, Post-hoc comparisons on the interaction, showed a significant difference in three color sequence pairs on the effect of the PSE, (Exp2-RR-Exp1-RB [$t = -3.653$, adjusted $p = .010$], Exp1-RB-Exp2-RB [$t = 3.383$, adjusted $p = .024$], and Exp1-RB-Exp2-BR [$t = 3.434$, adjusted $p = .023$]) (see Table 3.4.5). This interaction supports the fact that different equiluminant methods can result in differences in temporal perception.

Table 3.4.1: Descriptive results table of the PSE in both Color and Exp condition

Color	Exp	Mean	SD	N
Blue-Blue	Experiment 1	2.011	0.048	24
	Experiment 2	1.994	0.131	14
Red-Red	Experiment 1	2.016	0.046	24
	Experiment 2	1.953	0.136	14
Red-Blue	Experiment 1	2.058	0.072	24
	Experiment 2	1.961	0.112	14
Blue-Red	Experiment 1	1.970	0.078	24
	Experiment 2	2.024	0.066	14

Although the physiological models suggesting a differential effect of different PLR amplitudes on temporal perception are currently lacking, our newly found causality between the equiluminant method and temporal perception can be explained by neural intensity fluctuations based on the amount of incident light entering the pupil. The PLR generally controls pupil diameter to assist in vision adaptation via pupil constriction against intense ambient luminance and dilation in a dark environment. Therefore, the physical constriction of the pupil reduces the number and probability of photons captured by the retina. Notably, recent studies suggest that the PLR is not merely a reflex to brightness, but also affected by higher-order factors (Mathôt, 2018). As a matter of fact, pupil size also fluctuates according to hue (e.g., Szabadi, 2012; Herbst et al., 2011; Janisse, 1977), and even illusory brightness and subjectively perceived luminance (e.g., Laeng and Endestad, 2012; Sandoval Salinas et al., 2020; Binda et al., 2013). Furthermore, Kinzuka et al. recently reported that temporal perception is also modulated by the illusory

Table 3.4.2: Two-way repeated-measures ANOVA table on the effect of the PSE

Within Subjects Effects							
Cases	Sum of Squares	df	Mean Square	F	<i>p</i>	η^2	η_p^2
Color	0.012	3	0.004	0.492	0.689	0.010	0.013
Color * Exp	0.114	3	0.038	4.807	0.004	0.095	0.118
Residuals	0.851	108	0.008				
Between Subjects Effects							
Cases	Sum of Squares	df	Mean Square	F	<i>p</i>	η^2	η_p^2
Exp	0.033	1	0.033	6.205	0.017	0.027	0.147
Residuals	0.190	36	0.005				

Table 3.4.3: Simple main effects on Exp condition

Level of Color	Sum of Squares	df	Mean Square	F	<i>p</i>
BB	0.003	1	0.003	0.337	0.565
RR	0.035	1	0.035	4.314	0.045
RB	0.083	1	0.083	10.608	0.002
BR	0.026	1	0.026	4.884	0.034

Note. Type III Sum of Squares

Table 3.4.4: Simple main effects on Color condition

Level of Exp	Sum of Squares	df	Mean Square	F	<i>p</i>
1	0.093	3	0.031	6.561	< .001
2	0.045	3	0.015	1.111	0.356

Note. Type III Sum of Squares

Table 3.4.5: Post-hoc comparisons result for Exp \times Color condition

		Mean Difference	SE	t	Cohen's <i>d</i>	<i>p</i> _{bonf}
Exp.1, B-B	Exp.2, B-B	0.017	0.029	0.598	0.201	1.000
	Exp.1, R-R	-0.005	0.026	-0.195	-0.059	1.000
	Exp.2, R-R	0.058	0.029	2.013	0.677	1.000
	Exp.1, R-B	-0.047	0.026	-1.830	-0.552	1.000
	Exp.2, R-B	0.050	0.029	1.743	0.586	1.000
	Exp.1, B-R	0.041	0.026	1.604	0.483	1.000
	Exp.2, B-R	-0.014	0.029	-0.475	-0.160	1.000
Exp.2, B-B	Exp.1, R-R	-0.022	0.029	-0.773	-0.260	1.000
	Exp.2, R-R	0.040	0.034	1.206	0.476	1.000
	Exp.1, R-B	-0.064	0.029	-2.238	-0.753	0.750
	Exp.2, R-B	0.033	0.034	0.976	0.385	1.000
	Exp.1, B-R	0.024	0.029	0.839	0.282	1.000
	Exp.2, B-R	-0.031	0.034	-0.915	-0.361	1.000
Exp.1, R-R	Exp.2, R-R	0.063	0.029	2.188	0.736	0.849
	Exp.1, R-B	-0.042	0.026	-1.635	-0.493	1.000
	Exp.2, R-B	0.055	0.029	1.918	0.645	1.000
	Exp.1, B-R	0.046	0.026	1.799	0.542	1.000
	Exp.2, B-R	-0.009	0.029	-0.300	-0.101	1.000
Exp.2, R-R	Exp.1, R-B	-0.104	0.029	-3.653	-1.229	0.010
	Exp.2, R-B	-0.008	0.034	-0.230	-0.091	1.000
	Exp.1, B-R	-0.016	0.029	-0.576	-0.194	1.000
	Exp.2, B-R	-0.071	0.034	-2.120	-0.837	1.000
Exp.1, R-B	Exp.2, R-B	0.097	0.029	3.383	1.138	0.026
	Exp.1, B-R	0.088	0.026	3.434	1.035	0.024
	Exp.2, B-R	0.033	0.029	1.165	0.392	1.000
Exp.2, R-B	Exp.1, B-R	-0.009	0.029	-0.306	-0.103	1.000
	Exp.2, B-R	-0.063	0.034	-1.890	-0.746	1.000
Exp.1, B-R	Exp.2, B-R	-0.055	0.029	-1.913	-0.643	1.000

Note. P-value adjusted for comparing a family of 28

brightness of a glare illusion (a visual illusion that enhances perceived brightness without changing physical luminance) (Kinzuka et al., 2021), resulting in a different PLR response during the to-be-timed stimuli presentation (Zavagno et al., 2017; Suzuki et al., 2019b). In this study, the authors explained this probable temporal distortion mechanism as an internal magnitude decrease in the illusory brighter stimuli caused by the reduced light entering the eye from pupillary constriction. Recently, Suzuki et al. reported that the amplitude of SSVEPs decreased in accordance with constriction-eliciting stimuli (Suzuki et al., 2019a).

Moreover, they described this inhibition of SSVEPs as a causal relationship between illusion-induced pupil constriction and less light entering the pupil. These findings agree that the duration of red stimuli (relatively larger pupil diameter) was considered longer than blue (relatively smaller pupil diameter); the energy entering the eye was higher when the luminance of the stimuli was controlled by subjective (\equiv physical) equiluminance (Experiment 1). In fact, the pupil diameter at the PLR peak induced by the red stimulus was only approximately 60% of that induced by the blue stimulus.

Furthermore, Katsuura et al., who examined the effect of red and blue colors on temporal perception, reported that the cortical activity level in the visual pathway (retina-lateral geniculate body-primary visual cortex) might influence the temporal modulation effect, as mentioned earlier (Katsuura et al., 2007). Since other researchers noted that pupil constriction and less light entering the pupil could result in decreased activation in visual-related brain regions, this may cause temporal underestimation of the interval, an assumption based on the coding efficiency model (Eagleman and Pariyadath, 2009). In this model, Eagleman and Pariyadath proposed that neural coding efficiency and the degree of activation provide a basis for temporal perception. Several subsequent studies revealed that various non-temporal factors that lead to temporal overestimation also evoke larger neural responses (*e.g.*, Matthews and Meck, 2016; Noguchi and Kakigi, 2006). Despite the speculative relationship between the cortical activity level in the visual pathway and temporal perception, from these relations, the disappearance of temporal modulation can be explained by the indirect control of the internal magnitude of the to-be-timed stimuli by matching the PLR. In Experiment 1, the stimulus luminance was matched based on subjective and physical luminance. As is evident from Figure 3.2.5, PLR constriction was weaker for the red stimulus; that is, the neural activity in the visual pathway of red stimuli was considered larger than that of blue stimuli. According to the coding efficiency model, stimuli that induce more extensive neural activity are perceived to be displayed for a longer period of time; hence, the local activity evoked by the red stimulus can explain why it was perceived to be displayed for a significantly longer period than the blue stimulus. However, in the second control experiment, because the luminances of the two colors were individually

controlled to match the peak PLR amplitude, indirectly controlling the photons captured by the retina, it is possible that the temporal modulation may not have occurred. Although we cannot discount the hue-arousing effect on temporal distortion since we were not able to directly assess subjective arousal, the results from both experiments suggest another possible mechanism of how the hue of a visual stimulus can modulate temporal perception. The inconsistent results noted in Table 2.6.1 could be attributed to the challenge of controlling physical properties, which results in different PLR amplitudes.

Here, we will note few limitations to the study. First, temporal processing mechanisms may vary between sub-second (milliseconds) and supra-second (seconds to minutes) interval ranges (Näätänen et al., 2004; Lewis and Miall, 2003). Additionally, recent studies have suggested that the PLR profile differs in late components in response to a blue stimulus, as ipRGCs (which respond to blueish light) (Markwell et al., 2010) respond more slowly to light than rods and cones do. As this study was focused on the judgment of display intervals ranging from 1,600 ms-2,400 ms, the color effect and the implications of the PLR on temporal perception may differ in other temporal ranges. Second, the experimental environment may not have been stringently controlled because the two studies were conducted in different locations on different participant groups. Despite colorimetric calibration and baseline correction, we cannot entirely exclude the possibility that the luminance of the display or either room was not completely identical. As baseline pupil diameter constitutes various factors, some aspects, such as cognitive load (*e.g.*, difficulties in the duration-discrimination task) and pupil near response (*e.g.*, visual distance) might affect the pupil diameter during the task (Mathôt, 2018). These effects are considered negligible since we compared pupillary responses within each study and focused solely on the relative changes in pupil diameter. However, in future studies, eye-tracker models and experimental environments, including the participant group, should be controlled to analyze the pupil diameter baseline and directly compare the results within experiments.

In our analyses of psychometric functions and pupil diameter, our results showed that the perceived duration of red was overestimated compared to blue, even when the physical aspects of the stimuli were strictly controlled in subjectively (\cong physically) equiluminant conditions. However, this overestimation faded when the luminances of the two stimuli were matched based on the PLR amplitude. This causality between the equiluminant method and temporal perception may be due to the amount of incident light entering the pupil, leading to the modulation of different degrees of neural activation in visual-related regions. These results suggest another possible mechanism of temporal distortion by hue, in addition to the previously discussed hue-arousing effect. In addition, our results suggest that the pupillary response somehow plays a role in temporal perception from a phenomenological perspective. Although these links

remain speculative at present and require further consideration, incorporating neuroscientific approaches and discussion on theoretical frameworks, we believe that discovering this causal role may help clarify the inconsistent results of previous studies and further elucidate the underlying mechanisms of temporal perception.

4

The effect of glare illusion-induced perceptual brightness on temporal perception

A similar version of this chapter has been published as:

Yuya Kinzuka, Fumiaki Sato, Tetsuto Minami, & Shigeki Nakauchi. “Effect of glare illusion - induced perceptual brightness on temporal perception.” *Psychophysiology*, 58(9), e13851, 2021.

Figures reproduced under [journal guidelines](#) and [CC BY 4.0](#).

4.1 Introduction

Numerous studies have reported the occurrence of temporal illusions due to the physical magnitude of the stimulus by conducting temporal perception tasks with stimuli associated with different sensory inputs. For instance, a longer judged duration (temporal-overestimation) as a function of stimulus magnitude has been demonstrated by non-temporal stimulus attributes such as stimulus size ([Rammsayer and Verner, 2014](#); [Xuan et al., 2007](#)), auditory loudness ([Matthews et al., 2011](#)), stimuli velocity ([Makin et al., 2012](#)), visual contrast ([Benton and Redfern, 2016](#)), numerosity ([Vicario, 2011](#); [Xuan et al., 2007](#)), stimulus regularity ([Sasaki and Yamada, 2017](#)), or flicker frequency ([Herbst et al., 2013](#)) in the visual and auditory domains. Furthermore, these magnitude effects have been generalized to other modalities, such as the tactile, by electrical and vibrotactile stimulation ([Williams et al., 2019](#)).

Although many previous findings have generally indicated that the subjective duration of a given interval correlates positively with stimulus magnitude (“more-is-longer” account), it is equally important that this subjective duration is modulated as well by the relative and not absolute magnitude of the stimulus (Gomez and Robertson, 1979; Matthews and Meck, 2016). Gomez and Robertson showed that a large visual stimulus is judged as longer when compared to small objects, but only when object size varied within the session and participants could explicitly compare their sizes (Gomez and Robertson, 1979). This may be due to the fact that perceptual representations of the magnitude depend on the confluence of external stimulation and internal processing. For internal processing, the allocation of processing capacity, memory, and even mental effort are considered as factors modulating temporal perception through the final perceptual magnitude (Block and Gruber, 2014; Matthews and Meck, 2016). These interactions determine the final perceptual clarity, which can explain how increased stimuli intensity may lead to overestimating subjective temporal perception.

Interestingly enough, Ono and Kawahara reported the occurrence of temporal illusion by the Ebbinghaus illusion, an optical illusion of size perception (see Figure 4.1.1 for a general Ebbinghaus illusion (Titchener, 1901; Burton, 2001)). In this study, Ono and Kawahara asked the participants to categorize the duration of the Ebbinghaus illusionary-size-varied object, and to estimate the size of the perceived object.

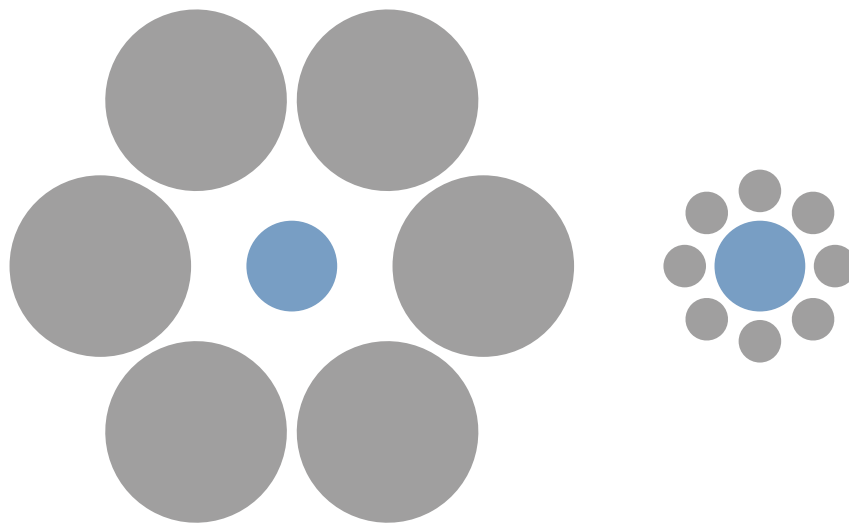


Fig. 4.1.1: The Ebbinghaus illusion (Titchener circles) (Titchener, 1901; Burton, 2001))

The two blue circles are exactly the same size; however, as a result of the juxtaposition of circles, the one on the right is usually perceived larger than the left.

The results showed that the perceived duration for subjectively larger circles (left blue circle for Figure 4.1.1) was longer than that of subjectively smaller circles (right blue circle for Figure 4.1.1), although both size of the circle remained invariant; furthermore, a bidirectionality effect was reported, where longer perceived stimuli were relatively perceived as larger (Ono and Kawahara, 2007). This straightforward result indicates the importance of the magnitude effect.

Non-temporal factors such as physical and perceptual stimulus magnitude are known to affect subjective temporal perception. However, most studies focusing on magnitude-related temporal illusions induced by stimulus magnitude so far assessed the effect of temporal illusions by presenting stimuli with relatively different physical intensities. Therefore, it remains unclear how perceptual magnitude itself directly affects temporal perception, and more direct evidence is required to understand how perceptual magnitude effects can be explained by the prominent temporal perception models/frameworks.

As luminance is one of the conspicuous magnitude dimensions in visual sensation, luminosity is one of the most focused non-temporal stimulus attributes part of a general principle that subjective duration is positively related to stimuli magnitude. The early scientific series of inquiries into the effect of stimulus luminance on perceived duration was conducted by Goldstone et al. The results showed that higher illumination can increase subjective perceived duration (Goldstone and Goldfarb, 1964; Goldstone et al., 1978), and was later replicated by several subsequent studies (Brigner, 1986; Long and Beaton, 1980). More recently, Xuan et al. investigated whether judgments of duration are modulated by magnitude information in various dimensions, such as space, quantity, and time. The results indicated that temporal accuracy was higher when luminance intensity and the to-be-measured duration were congruent in different temporal tasks, in other words, when the short-presented stimulus was dim, and the longer stimulus bright. Importantly, this congruency effect was found in different magnitudes (*e.g.*, number of dots, size of a square), indicating the existence of generalized and abstract components in magnitude representations (Xuan et al., 2007) (see section 2.7 for more details on the effect of luminance/brightness to temporal perception).

This prominent relationship between luminosity and subjective temporal perception is also reported to be affected by the relative, perceptual representations of luminance (Casini and Macar, 1997). Notably, absolute and relative stimulus brightness both predominantly affect temporal perception (Matthews et al., 2011). These recent studies raise the possibility that the perceptual representation of luminance magnitude, which modulates temporal perception, may also depend on the interplay between external stimuli intensity and cognitive internal processing. Therefore, clarification of whether and how the perceptual

intensity of brightness contributes to temporal perception should provide a key constraint on any model of the human perception of time.

To examine this topic, we combined the perceptual luminance magnitude effect on temporal perception and glare illusion stimuli during pupillometry recording. The glare illusion is an optical illusion in which we perceive the central region to be brighter regardless of the actual luminance in the center region (Figure 4.1.2) (Zavagno and Caputo, 2001; Zavagno, 1999; Agostini and Galmonte, 2002). The glare illusion is known as a robust illusion, with recent psychophysical studies showing that the illusion enhances the perceived magnitude of the brightness by 20% to 35% compared to the control stimuli (Tamura et al., 2016).

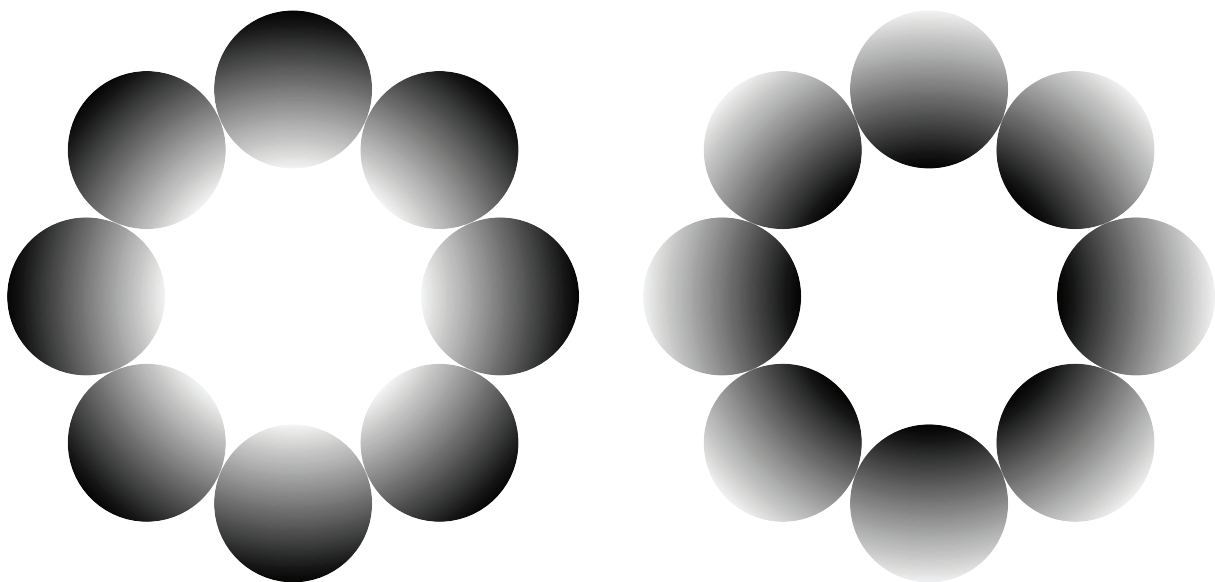


Fig. 4.1.2: Glare and Halo stimuli

The Glare illusion and halo stimuli. Both the glare illusion (left) and halo stimuli (right) consist of luminance gradient circles that either converges toward the pattern's center or toward the periphery (inducers). The central region of the glare illusion typically appears brighter than the background and the halo stimulus despite them being equiluminant. Note that the luminance in this figure differs from the stimuli used in our study.

Additionally, pupil diameter is known to reflect not just the physical luminance of the environment but various physiological internal states as well as the subjective brightness derived from the stimuli (Binda et al., 2013; Laeng et al., 2012; Mathôt, 2018). Accordingly, several studies have reported pupil diameter

to also reflect the perceptual brightness conveyed by the glare illusion, despite the physical luminance being identical to the control stimuli (Laeng and Endestad, 2012; Laeng et al., 2018; Suzuki et al., 2019a; Zavagno et al., 2017).

Therefore, in this study, we measured the perceived interval duration of visual objects whose perceived brightness was altered by the glare illusion while undergoing pupil diameter recording as an index of perceptual brightness. Additionally, the eye-movement recordings, which were simultaneously conducted with pupillary recording, enabled us to examine the effect of saccadic eye movements on temporal illusions since Morrone et al. reported that a saccade during visual stimuli presentation leads to temporal compression (Morrone et al., 2005). This experimental design aimed to examine whether temporal illusions occur by glare illusions, where physical intensity is identical while perceptual brightness differs (Experiment 1). In addition, a controlled study was conducted to clarify whether the temporal modulation effect happens only with illusory luminance and whether an actual physical luminance manipulation equivalent to the glare and halo also results in temporal illusions (Experiment 2). If the temporal perception process mainly relies on representation after the occurrence of the perceptual brightness illusion, the perceived interval duration of the glare illusion should be longer than that with halo stimuli due to the perceptual magnitude increment. If, however, the magnitude process is independent from the internal process, the perceived duration should remain the same since the physical luminance of both stimuli is identical. In other words, we hypothesized that the perceived duration of the glare illusion would be longer than with the halo stimuli due to the greater magnitude of internal representations.

4.2 Illusory magnitude on temporal perception (Experiment 1)

4.2.1 Introduction

In Experiment 1, glare illusion and a control stimulus were used as the to-be-timed stimuli in a temporal discrimination task to examine whether temporal illusions occur by glare illusion, where physical intensity is identical while perceptual brightness differs. This experiment mainly focuses on **Research question 2**, aforementioned in section 1.4.

4.2.2 Materials and methods

Participants

All experimental procedures and methods were in accordance with the ethical principles outlined in the Declaration of Helsinki and approved by the Committee for Human Research at the Toyohashi University

of Technology, and the experiment was strictly conducted in accordance with the approved guidelines of the committee. Informed written consent was obtained from participants after procedural details had been explained. The experiment involved 26 Japanese students (20 men, 1 women; age range: 21-25 years; $M = 21.70$, $S.D. = 1.20$) at the Toyohashi University of Technology. None of the participant's eye movement data were excluded from pupil analyses since the trial rejection ratio did not exceed the criteria of 50% after interpolation in the pre-processing phase. In the behavioral data analysis, trials where the reaction time (RT) > 10 s were excluded from analysis assuming low task performance. Only a limited proportion (0.13%) of trials were rejected by this criterion. All participants had a normal or corrected-to-normal vision and no participants reported color vision deficiency.

Stimuli and apparatus

The task was conducted in a shielded, darkroom using MATLAB 2016a (The MathWorks, Natick, MA, USA) and the MATLAB toolbox, Psychtoolbox 3 (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007), were used for stimulus presentation. The instructions and stimuli were presented on a liquid-crystal display (LCD) monitor (Display++, Cambridge Research Systems Ltd, Rochester, UK) with a resolution of $1,920 \times 1,080$ pixels and a refresh rate of 120 Hz. As we gave importance to the equivalence of physical stimulus properties, colorimetric and spectro-radiometric calibration was conducted in advance for linear light output (SR-3AR, TOPCON, Tokyo, Japan). The eye-tracker was placed below the presentation display, centered on the participant. The participant's head was placed on a chin rest at a viewing distance of 70 cm from the screen. All behavioral responses were performed using a numeric keypad with unnecessary keys removed.

In the temporal discrimination task, we used the glare illusion stimulus, which consists of an 8-circular pattern arranged in a circular shape with luminance gradations converging to the central white area and the halo stimulus with the reverse luminance gradient (see Figure 4.1.2 for an example of the glare/halo stimuli; Note that the luminance in the figure differs from the stimuli used in our study). The achromatic gradation of the circular pattern in both stimuli changed progressively from 0.74 to 82.09 cd/m^2 in luminance (i.e., the luminance on the inner and outer region of each circle was 82.09 and 0.74 cd/m^2 respectively for the glare stimuli), a result of selected RGB values ($R = 1.0, G = 1.0, B = 1.0$), ($R = 170.0, G = 170.0, B = 170.0$). The background and central region of stimulus luminance also remained constant at 54.17 and 82.09 cd/m^2 , respectively, in the achromatic color ($x = 0.3127, y = 0.329$ in the CIE1931 color space). Both stimuli were presented with a visual angle of 12.10 deg. During stimuli presentation, a small fixation cross was located in the center of the screen at a visual angle of 0.3 deg for

pupil diameter recording.

The pupillary response was recorded binocularly with an eye tracker (EyeLink 1000 Plus, SR Research, Oakland, Canada) at a sampling rate of 500 Hz. A five-point calibration was performed prior to each session of the duration discrimination task.

Procedure

The procedure of the duration discrimination task was based on a recent temporal perception study by Thönes et al. (2018), with 320 trials of a two-interval duration discrimination task conducted over four sessions. Figure 4.2.1A shows the protocol for one trial in each session.

The eye-tracker was calibrated prior to each session using a standard five-point calibration, each session lasting approximately 10 min. In the two-interval duration-discrimination task, either the glare illusion stimuli or halo stimuli were presented continuously on the screen followed by the 500 ms inter-stimulus interval (ISI). A fixation cross with a visual angle of 0.3 deg was continuously displayed at the center while eye-movement recordings were performed. On each trial, one stimulus was presented for 2,000 ms (reference interval; hereinafter called RI), while the duration of the other stimuli varied between 1,600 ms to 2,400 ms in five steps (comparison interval; hereinafter called CI); separated by a blank interval of 500 ms. After the presentation of the two stimuli, the participant indicated which stimulus had been presented for a subjectively longer duration by a numeric keypad, with “4” indicating the former stimuli and “6” for the latter stimuli (two-alternative forced-choice without an option to indicate equal duration). No feedback was provided. The order of temporal positions was randomized and counterbalanced across sessions using a within-subjects design. Figure 4.2.1B shows the combination of the 40 conditions in this study. Four different stimuli sequences were presented (glare-glare, glare-halo, halo-glare, halo-halo). The experimental condition was fully crossed by three experimental factors (stimuli sequence, CI position, and CI duration). Each condition was presented in 8 trials, resulting in a total of 320 trials per participant.

Prior to the main task, participants received a short practice session of randomly selected 10 trials, and sufficient breaks between the four sessions. Temporal judgment strategies such as counting-up or other rhythmic activity which are reported to increase temporal sensitivity (Grondin et al., 2004) were not specifically instructed, although their use was not restricted.

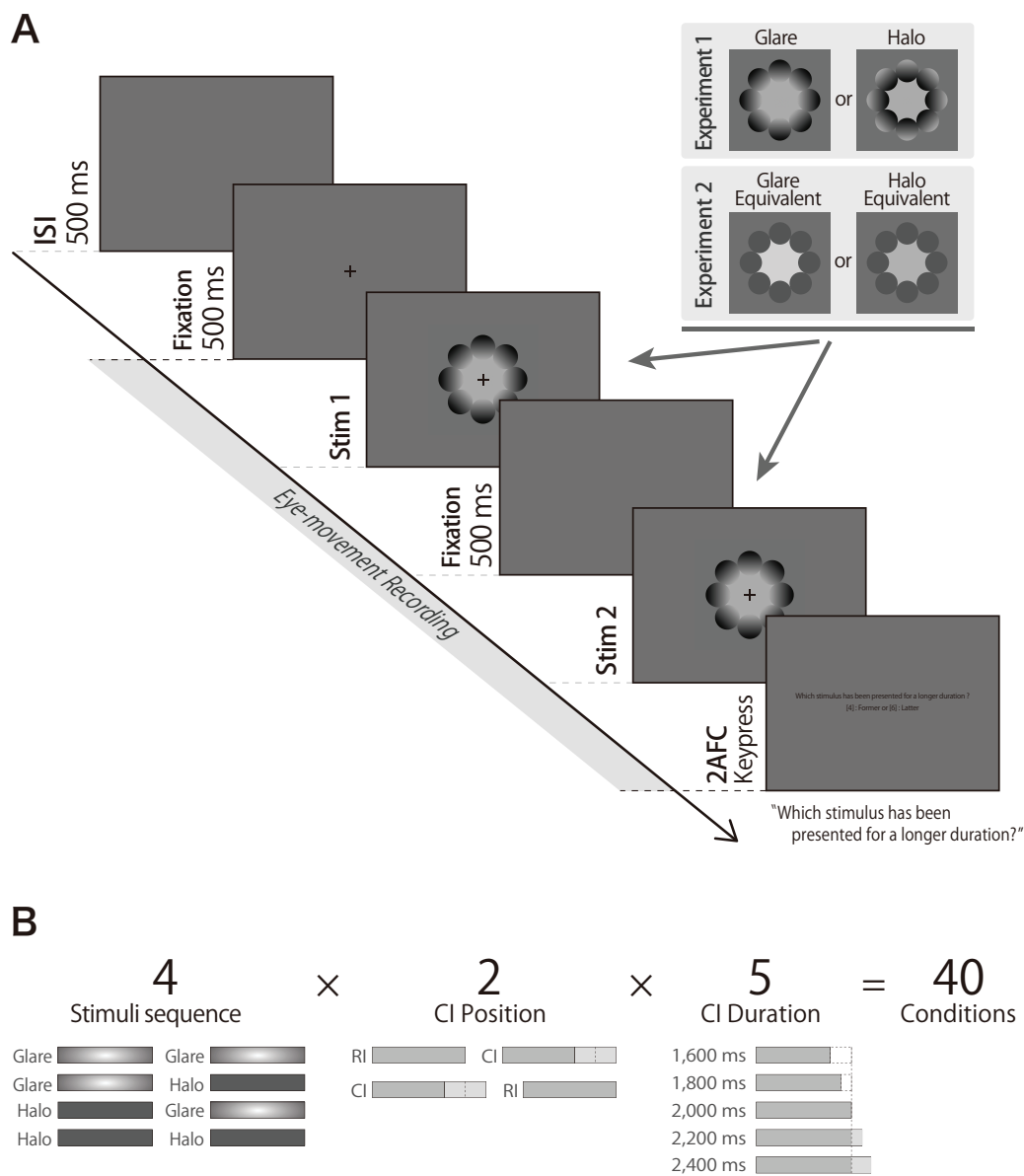


Fig. 4.2.1: Experimental protocol for one trial (Exp.1 & Exp.2)

(A) Sequence of one trial in the experiment. Stim1 and Stim2 refer to either the reference interval (RI) or comparison interval (CI). In Experiment 2, the two stimuli were replaced with subjectively equivalent uniform stimuli determined by an adjustment task. (b) Illustration of experimental conditions

Data analysis

The timing of blinks during eye movement measurements was not specified to the participants; thereby, blinks were interpolated before analysis using cubic-spline interpolation (Mathôt et al., 2013) in MATLAB 2018b. Trials that contained additional artifacts, computed by thresholding the peak changes in the velocity of the pupillary response were excluded from the analysis. Pupil size was generated by the eye-tracker device in arbitrary diameter units (EyeLink values). In the time-course analysis, the pupil diameter at stimulus onset in each trial was normalized relative to the baseline pupil size, following the smoothing of each data point with ± 10 sampling points. Baseline pupil size was derived as an average of data collected during the fixation period prior to each stimulus onset from -50 ms to 0 ms.

Saccades were detected by the velocity-based algorithm proposed by Engbert and Kliegl (2003), computed by MATLAB 2020b after blink detection. The onset and termination of each saccade were determined by the timing when gaze velocity exceeded 30 deg/s. The number of saccades per trial was normalized by the reference interval duration ($2,000$ ms). Bayes factor BF_{10} was computed by the Bayesian t -test as an indicator to interpret the effect of the null hypothesis on the saccade rate.

The proportion of CI stimuli judged longer was calculated from the responses at each duration CI step. To estimate psychometric functions, the responses for each individual were modeled by fitting the logistic psychometric function using Palamedes toolbox for MATLAB (Prins and Kingdom, 2018). Threshold and slope were set to free parameters, although if any of the psychometric functions for each stimulus sequence condition could not be fit accordingly, all data for the applicable participants were excluded from the subsequent statistical analysis. After psychometric function fitting, the model was then used to compute the point of subjective equality (PSE) and just noticeable difference (JND) for each stimuli sequence condition (G-G, G-H, H-G and H-H; “G” and “H” for glare and halo, respectively, representing the CI-RI combination). The PSE of the level of duration continuum at which the subjective temporal perception of the comparison stimuli is identical to the duration of the reference stimuli (RI), was computed to compare the effect of differences in perceptual brightness. R for Mac OS X version 3.5.1 and an analysis of variance function that runs on R language (anovakun version 4.8.2), was used for all statistical analyses. Pairwise comparisons of main effects were corrected for multiple comparisons using the Shaffer’s MSRB (Modified Sequentially Rejective Bonferroni (Seaman et al., 1991)) and the significance level was set to $p < .05$ for the analysis of variance (ANOVA). In the ANOVA, partial η (η_p^2) is reported as a measure of association strength (effect size). In addition, Bayes factor BF_{10} was computed by the Bayesian repeated-measures ANOVA as an indicator to interpret the effect of the null

hypothesis.

In addition, JASP 0.14.1 (JASP Team, 2019) was used to examine the direct and indirect effects in mediation analysis, implementing the bootstrapping procedure. The statistical significance of the mediating variable was investigated using 3,000 bootstrap samples to generate 95% confidence intervals of the indirect effects and examined if the interval is not straddling zero. Stimuli condition was used as a dummy variable (0: glare; 1: halo) and all regression coefficients were standardized.

4.2.3 Results

Duration judgment

In the two-interval duration discrimination task, participants were instructed to indicate the longer stimuli of either the RI (in which the duration is fixed to 2,000 ms) or CI (1,600 ms to 2,400 ms in steps of 200 ms). Each probability was used toward psychometric function fitting by each duration step of the CI to compute the PSE and JND. Figure 4.2.2 represents the mean psychometric function computed by the average of all participants with a longer CI proportion in each CI duration difference condition (duration difference was calculated by subtracting RI duration from CI duration).

In Figure 4.2.2, each solid line represents the fitted psychometric function. Each label indicates RI and CI stimuli, respectively (*e.g.*, H-G represents the RI stimuli being halo and the CI stimuli being glare). Dashed vertical lines represent the PSEs in each condition. The achromatic horizontal line at the bottom represents the domain with a significant difference as observed in the fitted function by *t*-test analysis, for reference purposes. Note that no statistical correction to account for multiple comparisons was performed in this *t*-test analysis. From the estimated psychometric function, a relative shift of the curve was observed in the incongruent stimuli comparison, whereas no shift was observed in the congruent stimuli comparison. The PSE and JND determined by the psychometric function are shown in Figure 4.2.3A, B, respectively.

Since CI position was not fixed and presented first or second with equal probability, a one-way repeated-measures ANOVA on the effect of stimuli sequence was performed. For the PSE, the effect of stimuli sequence was significant ($F[3, 60] = 5.1919, p = .0030, \eta_p^2 = 0.2061$), and therefore a post hoc *t*-test was also conducted. The post hoc analysis showed that the two incongruent stimuli sequences, H-G and G-H, significantly differed as the PSEs were smaller when the CI stimulus was halo rather than glare, $t_{20} = 3.2719$, adjusted $p = .0229$, whereas no other combination of stimuli sequences had

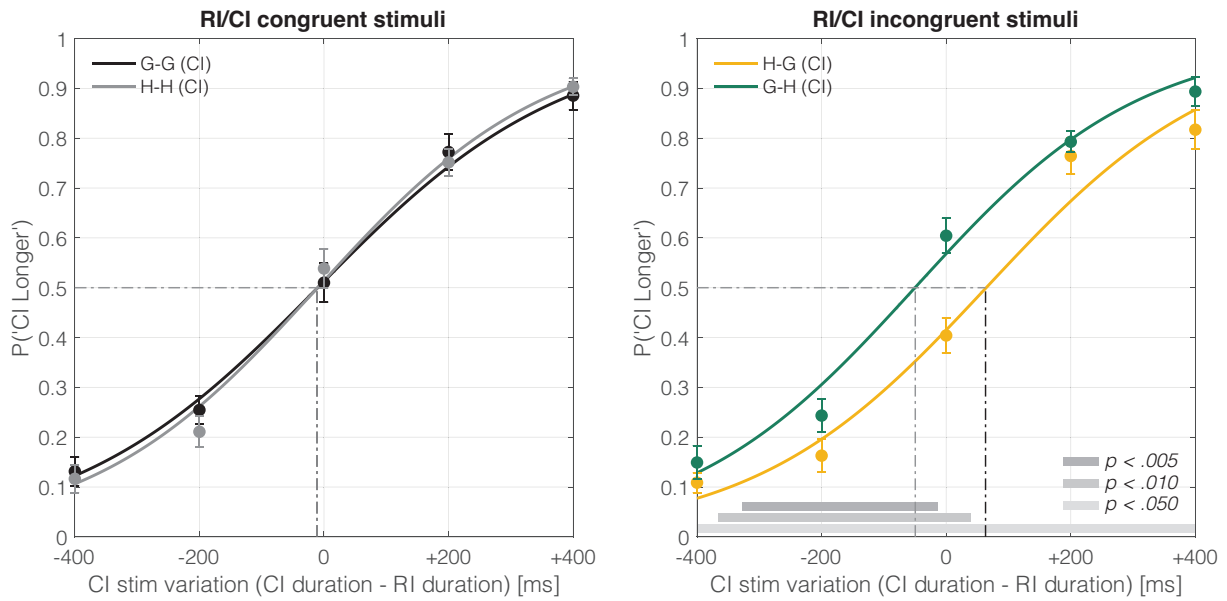


Fig. 4.2.2: Mean psychometric functions (illusory condition)

Left panel: Psychometric function fitting by the proportion of comparison interval-longer (CI) response in congruent color sequence. Right: Same as the left panel but for incongruent stimuli sequence. A rough indication of the significant t -test domain is shown at the bottom. CI, comparison interval; G, Glare; H, Halo; RI, reference interval.

significant differences. The shift of PSEs suggests an overestimation by halo stimuli compared with glare. Importantly, no overestimation was found in other stimuli sequences. In contrast to PSE, the main effect of stimuli sequence on JND, which is a measure of sensitivity, did not reach statistical significance ($p < .05$) and the effect size was relatively small ($F[3, 60] = 0.3087, p = .8190, \eta_p^2 = 0.0152$). Thus, we analyzed the present results with a Bayesian repeated-measures ANOVA to statistically conclude no difference in the JND. The analysis indicated Bayes factor $BF_{10} = 0.091$, which is smaller than $\frac{1}{10}$, providing strong evidence to support the null hypothesis (Ortega and Navarrete, 2017; Dienes, 2014). Importantly, the statistical analyses suggest no modulation of JND; in other words, temporal sensitivity did not differ by stimuli sequence.

Pupillary response

We tracked changes in pupil diameter as an index of the perceptual brightness conveyed by the stimuli. All trials of glare and halo stimuli in both RI and all CI duration were averaged across conditions. Figure 4.2.4A shows the grand average of the pupil responses during a -50 ms to $1,600$ ms stimulus onset under both stimuli (glare or halo) and duration (RI or CI) conditions.

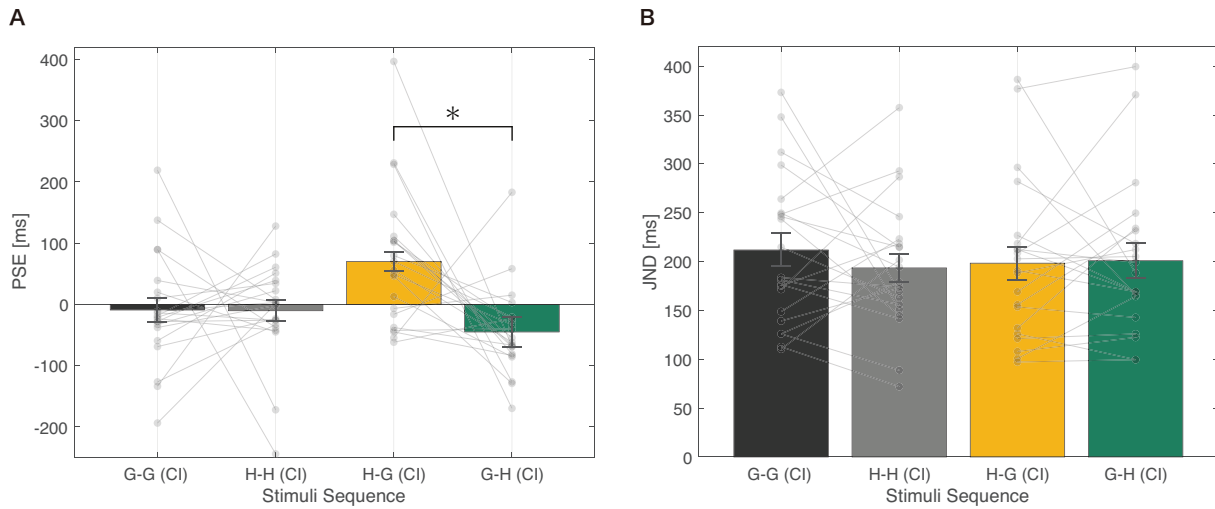


Fig. 4.2.3: Mean psychophysical function properties (illusory condition)

(A) Mean PSE as a function of stimuli sequence. (b) Mean JND as a function of stimuli sequence. Error bars in both figures indicate standard error of the mean. * Statistically significant ($p < .05$) differences in the analysis of variance and post hoc testing. The semi-transparent dot indicates the mean value for each participant data. CI, comparison interval; G, Glare; H, Halo; JND, just noticeable difference; PSE, point of subjective equality.

The profile of a typical orienting response (Wang and Munoz, 2015) and the pupillary light reflex (PLR) were observed from the pupillary response. The peak pupil diameter of the PLR is depicted in Figure 4.2.4B, computed by the average of minimum pupil diameter between 300 ms-1,300 ms in the time domain, given that PLR latency depends on the stimulus intensity, and has a peak generally around 500 ms (Ellis, 1981). As shown in Figure 4.2.4, the two-way repeated-measures ANOVA (stimuli condition \times duration condition) evaluating the effect of peak pupil diameter revealed a significant main effect on the stimuli condition ($F[1, 20] = 39.1142, p < .001, \eta_p^2 = 0.6617$). However, duration condition did not reach statistical significance ($F[1, 20] = 2.3175, p = .1436, \eta_p^2 = 0.1038$). Detailed ANOVA results are shown in Table 4.2.1.

The results indicated a larger PLR in association with the glare stimuli compared with halo stimuli. As shown in Figure 4.2.4A, the mean minimum pupil diameter of the PLR induced by the glare illusion was 1.71-times smaller than that by the halo stimuli. Assuming the pupil is a true circle, the pupil area at the PLR peak was only approximately 34% in association with glare stimuli compared to halo stimuli, despite the two stimuli being physically equiluminant.

Lastly, as with pupillary response analysis, the number of saccades was computed in all glare and

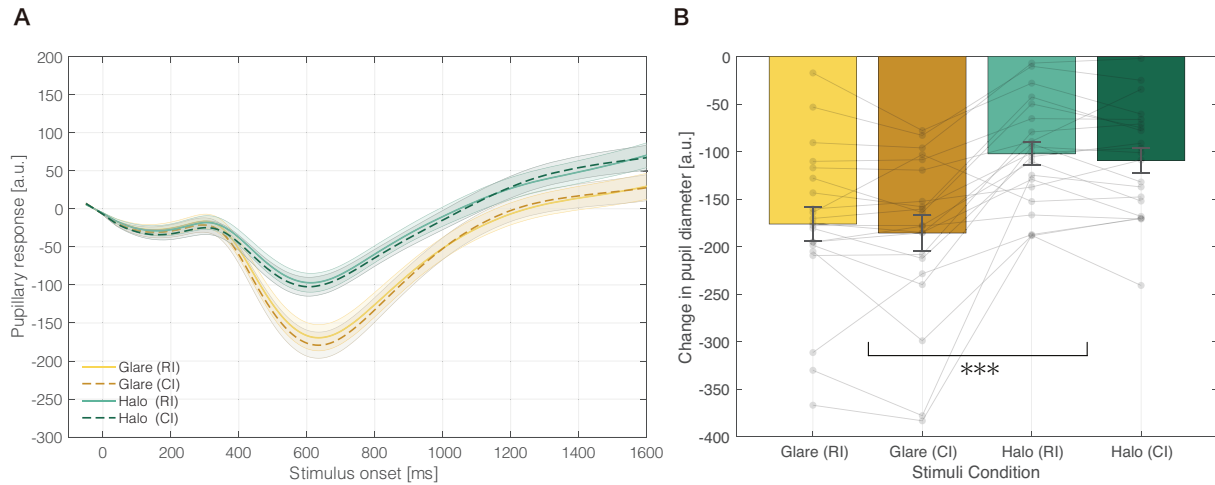


Fig. 4.2.4: Pupillary response to glare and halo stimulus

(A) Mean change in pupil diameter from stimulus presentation. Solid and dashed lines represent pupillary responses by RI and CI stimuli, respectively. Error bars are standard error of the mean. Note that the x -axis plot is limited to 1,600 ms, the shortest CI duration. (b) Mean PLR amplitude of each stimuli condition. PLR amplitude is computed as the minimum pupil diameter between 300 ms and 1,300 ms in the time domain. *** indicates statistically significant ($p < .001$) differences in the main effect of the ANOVA. The semi-transparent dot indicates the mean value for each participant data. ANOVA, analysis of variance; CI, comparison interval; PLR, pupillary light reflex; RI, reference interval.

Table 4.2.1: Two-way repeated-measures ANOVA table on the effect of the PLR amplitude

Within Subjects Effects							
Cases	Sum of Squares	df	Mean Square	F	p	η^2	η_p^2
Stimuli	118448.426	1	118448.426	39.114	< .001	0.584	0.662
Residuals	60566.175	20	3028.309				
Duration	1440.897	1	1440.897	2.317	0.144	0.007	0.104
Residuals	12438.922	20	621.946				
Stimuli * Duration	29.939	1	29.939	0.061	0.807	1.477×10^{-4}	0.003
Residuals	9756.399	20	487.820				

halo stimuli trials and then averaged across conditions. The average number of saccades per trial for glare and halo stimuli were 0.89 and 0.91, respectively. A paired samples t -test between the number of saccades detected within the two stimuli conditions did not reach statistical significance ($p < .05$) and the effect size was relatively small ($t[20] = -0.917, p = .370$, Cohen's $d = -0.200$). Thus, we analyzed the present results with a Bayesian paired samples t -test, finding no difference in the saccade rates. The analysis indicated a Bayes factor $BF_{10} = 0.331$, providing moderate evidence to support the null hypothesis (Ortega and Navarrete, 2017; Dienes, 2014).

Mediation analysis

Results of the mediation analyses are presented in Table 4.2.2, and the model diagram is shown Figure 4.2.5. The standardized regression coefficient between stimuli (glare/halo) and PLR peak, computed by the minimum pupil diameter between 300 ms-1,300 ms time domain, was significant, as was the standardized regression coefficient between PLR peak and PSE.

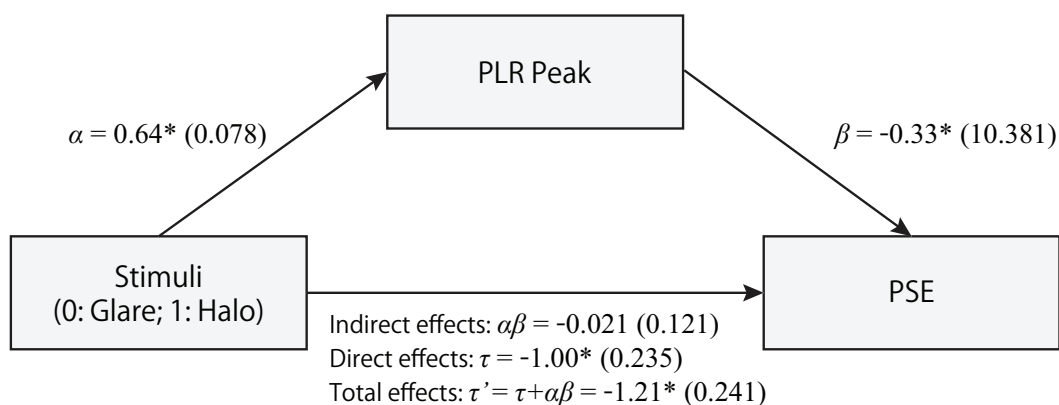


Fig. 4.2.5: Schematic diagram of mediation analysis results

Depicted is the path diagram including regression coefficients of total and mediated effects of stimuli (glare/halo) on the PSE. Path values are standardized regression coefficients for the relationship with standard errors in parentheses. * indicates statistically significant ($p < .05$). PLR, pupillary light reflex; PSE, point of subjective equality.

The significance of this indirect effect was evaluated using bootstrapping procedures. For each, 3,000 bootstrapped samples were used, and the 95% confidence intervals (CI) of the indirect effects were computed by determining the indirect effects at the 2.5th and 97.5th bias-corrected percentiles. Path a and path b showed a significant regression; however, the bootstrapped indirect effect did not reach statistical

Table 4.2.2: Mediation analysis result - parameter estimates

Direct effects							
		Estimate	Std. Error	z-value	p	95% CI	
						Lower	Upper
Stimuli →	PSE	−0.999	0.235	−4.254	< .001	−1.509	−0.566
Indirect effects							
		Estimate	Std. Error	z-value	p	95% CI	
						Lower	Upper
Stimuli→	PLR → PSE	−0.210	0.121	−1.731	0.083	−0.590	−0.015
Total effects							
		Estimate	Std. Error	z-value	p	95% CI	
						Lower	Upper
Stimuli →	PSE	−1.209	0.241	−5.013	< .001	−1.689	−0.762

Note. Delta method standard errors, bias-corrected percentile bootstrap CI.

significance ($\alpha\beta = -0.021, p = .083$), the 95% confidence interval ranged from -1.509 to -0.566 , which did not include zero. A significant negative direct effect of stimuli on PSE was observed (Total effects; $\tau' = -1.21, p < .05$). In addition, when the PLR peak was included as the mediator in the analysis, this coefficient was reduced but still statistically significant (Direct effects, $\tau = -1.00, p < .05$).

4.2.4 Discussion

In this experiment, we investigated whether the temporal illusion of a visual stimulus is affected by the magnitude of perceptual brightness. Based on the prominent effects of magnitude on temporal illusions and a possibility that perceptual magnitude representations depend on the confluence of external stimulation and internal processing, one of our hypotheses was that the perceived interval duration of the glare illusion may be longer than that for halo stimuli due to the perceptual magnitude increment.

By means of a two-interval duration-discrimination task of glare and halo stimuli in the sub-second range, psychometric function fitting was performed. Based on the analysis of psychometric functions, the mean difference in the PSE suggests that glare and halo stimuli were perceived to be of equal duration when glare stimuli were in fact physically 115 ms (5.7%) longer than halo stimuli, contrary to the initial hypothesis (see Figure 4.2.3A). In contrast, no difference was found in the JND (see Figure 4.2.3B).

Additionally, no significant difference was found in the saccade rate between glare and halo stimuli, assessed to rule out the possibility that different stimulus-induced saccade rates caused the temporal illusion (Morrone et al., 2005). The mediation analysis was conducted to further discuss the relationship between the temporal illusion effect and pupillometry response. Individual regression was significant; however, we did not find significant evidence for an indirect effect. In addition, we could not fully segregate the effect of illusory increased magnitude and equivalent magnitude increase by physical luminance manipulation on temporal illusions.

4.3 Illusory magnitude matched (Experiment 2)

4.3.1 Introduction

The findings in Experiment 1 showed that temporal perception is influenced by the illusory brightness of glare stimuli. Therefore, to further focus on the effect of illusory luminance, physical luminance of the stimuli was manipulated to match the illusory-induced magnitude. This was to a.) confirm that the apparent magnitudes of glare and halo do actually differ by the stimulus used in experiment 1, and b.) to clarify whether the temporal compression effect happens only with the illusory luminance and not physical luminance difference. This experiment mainly focus on the explication of **Research question 2** and **Research question 3** (see section 1.4).

4.3.2 Materials and methods

Participants

In experiment 2, 20 Japanese students (20 men; age range: 22-26 years ($M = 22.8$, $SD = 1.00$)) were enrolled; six of these students had also participated in Experiment 1. In the behavioral data analysis, trials where the reaction time (RT) > 10 s were excluded from the analysis assuming low task performance (0.02% of the trials were rejected). All participants had normal or corrected-to-normal vision and no participants reported color vision deficiency.

Stimuli and apparatus

The task was conducted in the same shielded darkroom using MATLAB 2018b (The MathWorks, Natick, MA, USA) and a MATLAB toolbox, Psychtoolbox 3 mentioned in Experiment 1. Glare and halo stimuli, sharing the same physical properties as those in Experiment 1, were used only in the adjustment task to compute the subjectively equiluminant uniform stimuli. The uniform stimulus consisted of an 8-circular pattern (inducers) arranged in a circular shape identical to the glare/halo stimuli, except with a

uniform luminance distribution of 39.88 cd/m^2 , a result of the mean RGB values used for the inducers of glare/halo stimuli ($R = 85.5, G = 85.5, B = 85.5$). The central region of the uniform stimulus luminance ranged from 44.31 to 114.28 cd/m^2 based on the staircase method in the adjustment task in achromatic color ($x = 0.3127, y = 0.329$ in the CIE1931 color space). All glare, halo, and uniform stimuli were presented with a visual angle of 12.10 deg throughout the experiment. Target (glare or halo) and uniform stimuli in the adjustment task were horizontally shifted at 7.70 deg degrees each from the center of the screen.

Procedure

The procedure of the duration discrimination task was identical to Experiment 1. However, the to-be-measured stimuli were replaced with subjectively glare/halo-equivalent uniform stimuli (see Figure 4.2.1 for one trial protocol).

To clarify whether the temporal illusion happens by illusory luminance, a behavioral luminance adjustment task was conducted in advance of the main duration discrimination task. In the adjustment task, a 2AFC (Two-alternative forced-choice) staircases method procedure was adapted to determine a subjectively-equiluminant-luminance-value of glare and halo, respectively, for the center region of the uniform stimuli. Each trial in the adjustment task consisted of the presentation of the central fixation cross for 500 ms, followed by a simultaneous presentation of the target (glare or halo) and uniform stimulus for 3,000 ms. Subsequently, the participant reported whether the uniform stimuli were perceived brighter than the target (glare/halo) stimuli by using a numeric keypad. Based on the response and staircase procedure, the central region of the uniform stimulus luminance ranged ± 75 RGB values from the baseline luminance of glare/halo (170 RGB value) in a step of 3 RGB values (approximately 1.40 cd/m^2) per response. Trials of the staircase procedure were terminated when the number of reversals reached 8 times, or if the computed stimulus level continuously reached the limit for 3 times. Glare and halo were presented in 3 staircase trials, resulting in a total of 6 staircase trials per participant. The average of the final stimulus level was used toward the center region of the uniform stimuli in the duration discrimination task. The stimuli position was counterbalanced across participants, target stimuli order and initial stimuli level were randomized across trials using a within-subjects design. Prior to each task, participants received a short practice session of randomly selected 10 trials and sufficient breaks between the tasks and the four sessions in the duration discrimination task.

Data analysis

All aspects of data analysis in duration judgment were analogous to Experiment 1. In addition to the temporal perception analysis, average adjusted luminance in the adjustment task was analyzed to compare the apparent magnitudes of the stimuli used in Experiment 1. The grand average of adjusted luminance was computed by the mean of each final stimulus level in the two conditions (glare and halo), and then averaged across participants. Finally, a paired sample t -test was conducted on JASP 0.14.1 (JASP Team, 2019).

4.3.3 Results

In the adjustment task, the luminance of the center area in the uniform stimuli was manipulated to match the subjective brightness of glare and halo stimuli. Figure 4.3.1 shows the distribution of the applied luminance value.

The mean luminance value for glare and halo was 203.1 ($S.D.$ = 28.3) [RGB Value] and 177.9 (11.0) [RGB Value], respectively, and significantly different by a paired sample t -test ($t[19] = 4.617, p < .001$, Cohen's $d = 1.032$) with a relatively large effect size.

The PSE and JND to the glare/halo-equivalent stimuli sequence in the duration judgment task are shown in Figure 4.3.2A, B, respectively.

Again, a one-way repeated-measures ANOVA on the effect of stimuli sequence was performed. Contrary to Experiment 1, both the effect of stimuli sequence on PSE and JND did not reach statistical significance (PSE: $F[3, 57] = 0.543, p = .655, \eta_p^2 = 0.028$, JND: $F[3, 57] = 0.611, p = .611, \eta_p^2 = 0.031$). Therefore, we analyzed the present results with a Bayesian repeated-measures ANOVA and found no significant differences in the PSE and JND. The analysis indicated $BF_{10} = 0.134$ and $BF_{10} = 0.128$ for PSE and JND, respectively, both smaller than $\frac{1}{3}$, providing moderate evidence to support the null hypothesis (Ortega and Navarrete, 2017; Dienes, 2014). The statistical analyses suggest apparent duration and temporal sensitivity of the stimuli did not differ by stimuli sequence.

4.3.4 Discussion

In this second experiment, we conducted a duration discrimination task identical to Experiment 1, without eye-tracking and stimuli replaced with the equivalent uniform stimuli to clarify whether the temporal compression effect happens with illusory luminance. The behavioral results from the

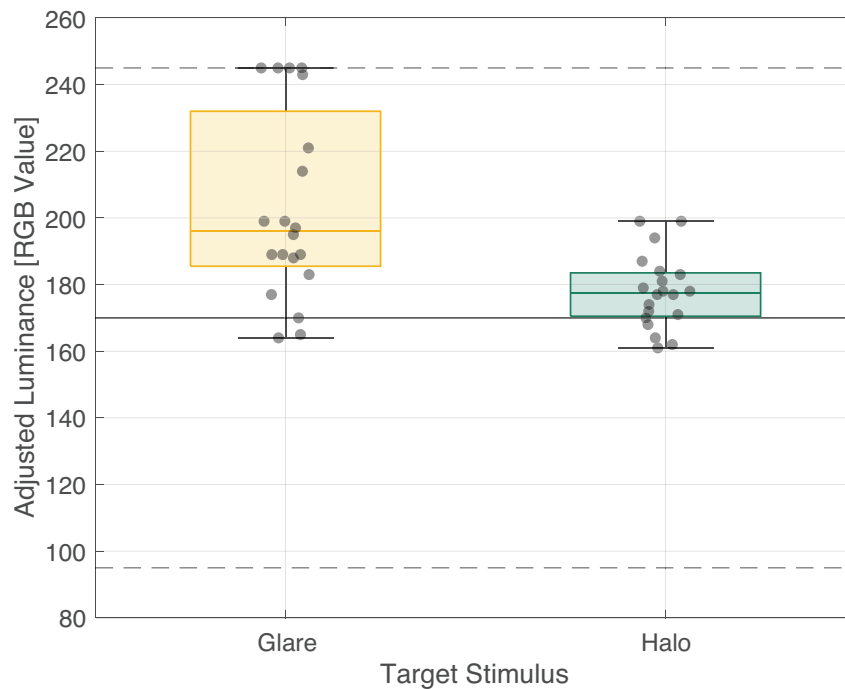


Fig. 4.3.1: Mean adjusted luminance equivalent to glare/halo stimulus

Box plot of the mean determined RGB value for glare and halo stimulus. The central line in each box represents the median value and the box shows the interquartile range (the 25th percentile to the 75th percentile). The whiskers reflect the minimum and maximum. Upper and lower dashed and solid horizontal lines represent the limit of the staircase procedure and physically equiluminant value, respectively. The semi-transparent dot indicates the mean value for each participant data.

adjustment task suggest that even though the luminance contrast of the glare stimuli used in this study was relatively low, the glare illusion was approximately perceived 14% brighter in physical luminance than halo stimuli (see Figure 4.3.1), as in previous reports (Agostini and Galmonte, 2002; Tamura et al., 2016). Furthermore, no difference was found in the PSE and JND (see Figure 4.3.2). However, this result contradicts previous studies considering that the perceptual representation of luminance can also influence perceived duration as explained in the “more-is-longer” account (*e.g.*, Casini and Macar, 1997; Matthews et al., 2011). This effect can be simply due to the slight luminance difference of the glare and halo-equivalent stimuli. In fact, the mean luminance difference of the center area was approximately 11.6 cd/m^2 , which is notably smaller than that obtained by previous studies conducted on a display or a tachistoscope (*e.g.*, Matthews et al. (2011): 96.2 cd/m^2 , Brigner (1986): 214.4 cd/m^2). These results suggest that a physical luminance matched to the illusory-induced magnitude is not sufficient to activate significant temporal modulation.

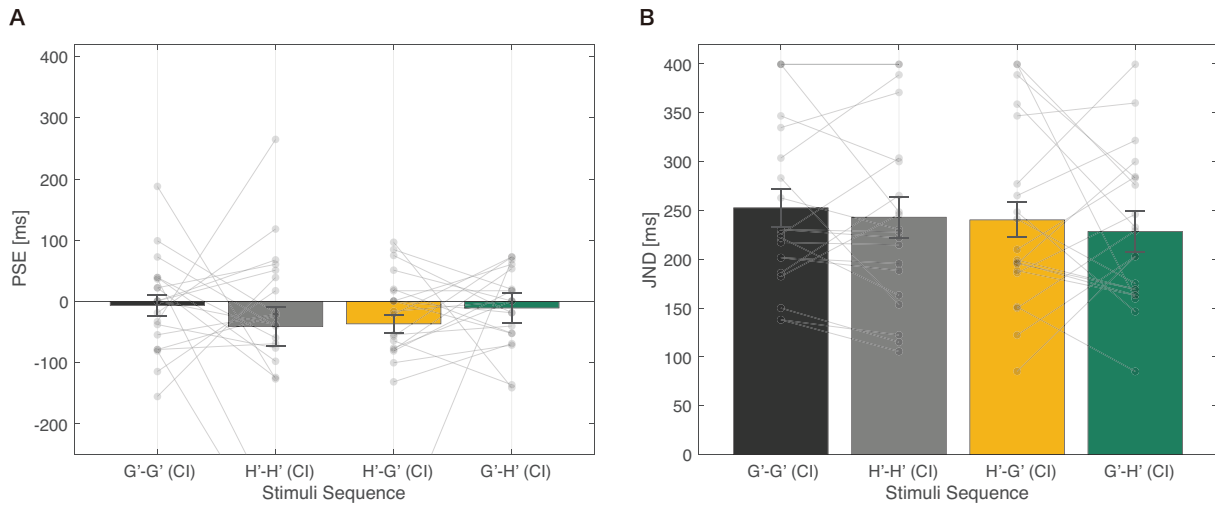


Fig. 4.3.2: Mean psychophysical function properties (illusory-magnitude matched condition)

(A) Mean PSE as a function of stimuli sequence. (b) Mean JND as a function of stimuli sequence. Error bars in both figures indicate standard error of the mean. * Statistically significant ($p < .05$) differences in the analysis of variance and post hoc testing. The semi-transparent dot indicates the mean value for each participant data. CI, comparison interval; G', Glare-equivalent; H', Halo-equivalent; JND, just noticeable difference; PSE, point of subjective equality

4.4 Discussion

In this study, we investigated whether the temporal illusion of a visual stimulus is affected by the magnitude of perceptual brightness rather than the physical magnitude of the luminance. In Experiment 1, we found that the glare illusion, which enhances apparent luminance, can evoke temporal modulation. In addition, Experiment 2 was conducted to clarify whether the temporal modulation effect happens only with illusory luminance. A PSE shift was not confirmed: an actual physical manipulation of luminance equivalent to the glare and halo did not activate significant temporal illusion. These results suggest stimuli with the same physical magnitude of luminance can evoke different subjective durations depending on how the stimuli-related magnitude is perceived. In other words, although temporal illusions were observed by physically equiluminant stimuli, contrary to the widely reported “magnitude effect”, the perceptual time of glare stimuli relative to halo stimuli was underestimated.

One explanation for this opposing glare stimuli-associated underestimation in terms of the prominent magnitude effect is that the magnitude of the internal representation induced by the glare may decrease due to greater pupil constriction, thereby reducing the amount of incident light entering the pupil. Since our pupillary response is generally a function of retinal illuminance controlling the physical input

from the ambient environment, the number and probability of photons captured by the retina decrease when the pupil is constricted even by glare illusions (Binda et al., 2013). In fact, the pupil area at the PLR peak induced by the glare stimuli was only approximately 34% in comparison with the halo stimuli, despite the physical equiluminance. Recently, Suzuki and colleagues reported that the amplitude of steady-state visual evoked potentials (SSVEPs), electroencephalography (EEG) signals representing feature-selective attention positively correlated with visual stimulus clarity, and surprisingly decreased in association with the glare illusion compared to control stimuli (Suzuki et al., 2019a). Furthermore, the study described the probable mechanism of this inhibited SSVEP as a causal relationship of glare illusion-induced pupil constriction in the primary stages of visual processing and the decrease of light entering the pupil. Similarly, Bombeke et al. also suggested that pupil diameter differences directly modulate the magnitude of the feedforward response of V1 (Bombeke et al., 2016). Moreover, with respect to the retinal illuminance increase, a very recent study by Sulutvedt et al. reported even slight pupil dilations due to the act of Tropicamide (a medication used for pupillary dilation) treatment can result in an enhanced perceptual brightness (Sulutvedt et al., 2021).

Since our perceptual representations of magnitude depend on the interaction between external stimulation and internal processing (Matthews and Meck, 2016), our results suggest the possibility that glare stimuli were perceived as shorter than halo stimuli, where the subjective magnitude decrease of glare stimuli was due to the constant pupillary constriction and was associated with a decrease in incident light entering the eye. Furthermore, our results and recent findings indicating the correlation between neural activities and pupil constriction may provide another explanation for temporal illusions through the well-known temporal model, the coding efficiency model (Eagleman and Pariyadath, 2009). In this model, Eagleman and Pariyadath proposed that neural coding efficiency offers a basis of subjective time and pointed out various non-temporal factors which expand perceptual duration also evoke larger neural responses (*e.g.*, Matthews and Meck, 2016; Noguchi and Kakigi, 2006). Since glare stimuli are known to evoke lower EEG signals and responses of V1 due to the greater pupillary constriction, according to this model, halo stimuli may result in temporal overestimation by relatively larger neural activity. In other words, the temporal compression by the glare stimuli can be explained by the secondary effect of the pupillary constriction on the coding efficiency model, resulting in less neural activity in visual areas. Furthermore, the temporal illusion effect by the halo stimulus is assumed to be relatively weak, since its sensory magnitude is low compared to that of the glare stimulus, which has a reverse luminance gradient not inductive of brightness enhancement illusion and conspicuous pupillary constriction. Importantly, the perceived magnitude is also reported to positively relate to the apparent duration regardless of changes in physical magnitude. Considering coding efficiency model into account, a study by Murray et al. found

that illusionary stimuli to be perceived as larger evoked greater cortical activity in V1 (Murray et al., 2006); this may explain the results by Ono and Kawahara that found that the same physical magnitude can extend subjective duration by illusionary larger objects (Ono and Kawahara, 2007), which also supports the supposition that subjective magnitude itself is sufficient to induce temporal illusions and explain the context-dependency of non-temporal effects on temporal perception. However, although Ono and Kawahara consider that temporal perception is also influenced by later processing related to visual illusions, considering bidirectional interactions in visual processing (Di Lollo et al., 2000), and the neural activity alteration resulting from pupillary constriction (Bombeke et al., 2016; Suzuki et al., 2019a), the perceptual stage involved in temporal illusions is still speculative.

Some study limitations should be noted. First, there is a possibility that glare underestimation could be due to the stimuli' local contrast difference. Despite the fact each element used in the glare and halo stimuli is identical and the mean physical luminance is equiluminant, due to the angle of the luminance gradations halo, stimuli may have a larger visual contrast in the fovea. Benton and colleagues conducted a study to evaluate the effect of contrast on perceived duration, since neural activity in early visual areas is related to contrast (Benton and Redfern, 2016); they reported that an increase, in contrast, is related to temporal overestimation; however, the temporal illusion effect was relatively small. In our current study, a fixation cross was located in the center of the screen for pupillometry recording. Therefore, while the main stimuli were relatively small (12.10 deg), participants could overestimate halo stimuli compared to the glare by the central stimulus contrast. Further, due to the ambiguous border by the stimulus gradient, we cannot fully deny the possibility that apparent size differed from the stimuli. Additionally, temporal illusions are often explained in terms of the attention state to the stimuli, since the increase of selective attention in temporal tasks is known to be associated with temporal sensitivity (Grondin et al., 2014). However, our analysis suggests no JND modulation in temporal judgments; thus, the effect of the contrast and attention process derived by the illusion is assumed to be relatively limited.

Second, the mechanisms of temporal processing are known to vary between sub-second (milliseconds) and supra-second (seconds to minutes) interval ranges (Lewis and Miall, 2003; Näätänen et al., 2004); since working memory is important for temporal processing such as duration comparisons of supra-second intervals (Lee et al., 2009), the timing of sub-second intervals are assumed to be a relatively automatic process and beyond cognitive control. Therefore, to further elucidate the perceptual magnitude effect by visual illusions in the early stages of visual processing, investigation in the sub-second range should also be taken into consideration. Third, this study has focused on the temporal distortion and pupillary response by visual stimuli. However, the pupillary response is known to reflect many other cognitive factors since

pupil diameter is determined by antagonistic activation in the autonomic nervous system (comprising the sympathetic and parasympathetic nervous system; Mathôt (2018)) and used as an indirect measure of activity in the locus coeruleus (LC), a brainstem nucleus involved in noradrenergic transmission (Mathôt, 2018). Considering this antagonistic effect, the increase in parasympathetic activity due to the pupillary constriction induced by the glare illusion may decrease sympathetic activity, which is associated with arousal, resulting in temporal compression by the glare stimuli. In addition, since some studies focused on the correlation between neuromodulation of the pupil size, the extent of LC activation, and subjective temporal perception in non-human primates (Faber, 2017; Suzuki et al., 2016), further interdisciplinary considerations incorporating both psychology and neuroscience approaches will be needed to yield any fundamental findings to deconstruct the complex neurobiological process and the role of the LC and pupillary response on temporal perception.

In conclusion, based on the analysis of psychometric functions, mean difference in the PSE and pupil diameter, our results are the first to demonstrate that temporal perception is also influenced by illusory brightness in glare stimuli, indicating the possibility that temporal processing depends on the confluence of both external magnitude and perceived subjective magnitude. In our study, pupillary response was recorded as an index of perceptual magnitude, since pupil diameter (*e.g.*, PLR) is known to reflect subjective brightness derived from the stimuli. The perceived duration of glare stimuli (apparently brighter; larger PLR) was shorter than that of halo stimuli (control stimuli), although the physical luminance remained equiluminant. This surprising temporal illusion by glare stimuli contrasts with the well-known magnitude model assuming the positive correlation of the subjective duration of a given interval with stimulus magnitude. However, this inconsistency may be explained by the subjective magnitude decrease of glare stimuli due to the constant pupillary constriction decreasing the light energy entering the eye, consistent with the coding efficiency model by Eagleman and Pariyadath (Eagleman and Pariyadath, 2009). As glare stimuli evoked a greater pupil constriction resulting in an over 60% decrease in pupil area compared to halo stimuli, EEG signals and V1 responses may also decrease, thus replicating previous studies that lead to glare stimuli's temporal illusion. However, these links remain speculative at present and further studies regarding the relationship between pupillary responses including incident light amount and perceived duration are required.

5 | Conclusion

The effects of various representations of stimulus magnitude on temporal perception were evaluated during the course of this thesis through the experiments in chapter 3 and 4. This approach not only addressed a new perspective on the two prominent targets of studies in temporal perception and the relation between temporal distortion by color and luminosity but also explained how pupillary response is involved in this relationship.

In particular, we first examined the potential effect of color (especially red vs blue) on temporal perception under careful stimuli control and tested if different equiluminant methods result in different temporal illusions in chapter 3. We then investigated whether subjective magnitude itself is sufficient to induce temporal illusions and how PLR amplitude is involved in temporal perception (chapter 4), which are all the constituents of the research question stated in section 1.4. In this section, the findings and contributions of the study will be summarized, and we will describe how the findings can impact further research in the field.

5.1 Summary

Effect of color on temporal modulation under different equiluminant conditions

In chapter 3 the goal was to answer the first two research questions of the study: *What is the potential effect of color (especially red v.s. blue) on temporal perception under careful stimuli control?* and *What is the relationship between pupillary response and temporal perception?*. Although the ubiquity of color has been driving research on the potential effects of the colors, the results have been inconsistent (shown in Table 2.6.1), which could be attributed to the difficulty of controlling physical properties such as hue and luminance within and between studies. Therefore, we conducted a two-interval duration-discrimination task to evaluate the perceived duration of color stimuli under different equiluminant conditions: subjective or PLR-based equiluminance. The results, based on psychometric functional analyses and simultaneous pupillary recordings, showed that the perceived duration of red was overestimated compared with blue, even when the intensity of the stimulus was controlled based on subjective equiluminance and primarily

by physical luminance too (Experiment 1). However, since blue is known to induce a larger PLR than red despite the physical equiluminance, a controlled study was conducted to distinguish the indirect effect of pupillary response on temporal perception. Interestingly, the effect observed in Experiment 1 faded when the luminance levels of the two stimuli were matched based on the PLR response (Experiment 2). These results indicate that duration of the judgment can be affected not only by the hue but by different equiluminant methods.

Effects of various representations of stimulus magnitude on temporal perception

Since stimulus magnitude is assumed to be positively related to the perceived duration from the early days of experimental psychology, most studies have assessed this effect by presenting stimuli with relatively different intensities in physical quantity. However, in response to the plausible fact that different equiluminance-method-based-control can result in different effects on temporal duration, we next examined how internal magnitude is involved (chapter 4). In this chapter, the main research questions were, *Is subjective magnitude itself sufficient to induce temporal illusions when the physical intensity is identical?* and *What is the relationship between pupillary response and temporal perception?*. In this study, we conducted another two-interval duration-discrimination task and adopted a glare illusion (a visual illusion that enhances perceived brightness without changing the physical luminance) to investigate whether the temporal perception is also influenced by the perceptual magnitude. Based on the mean difference in the point of subjective equality derived from a psychometric function and pupil diameter, we found that temporal perception is influenced by the illusory brightness of the glare stimuli.

Interestingly, the perceived duration of the apparently brighter stimuli (glare stimuli; larger PLR) was shorter than that of control stimuli (halo stimuli; smaller PLR) despite the stimuli remaining physically equiluminant, in contrast with the well-known "magnitude effect." Furthermore, this temporal modulation did not occur when the physical luminance of the stimuli was manipulated to match the illusory-induced magnitude. These results indicate that temporal processing depends on the confluence of both the external and perceived subjective magnitude as the illusory brightness is also sufficient to affect the sense of duration; which may be explained by the internal magnitude decrease of the glare stimuli due to pupillary constriction decreasing the amount of incident light entering the eye.

5.2 General discussion

Table 5.2.1 summarizes the results of all four experiments, including which aspects of stimulus-magnitude-representations were matched, and the occurrence of the temporal distortion within the stim-

ulus condition.

Table 5.2.1: Summary of the studies

	Exp	Stimulus	Saturation	Luminance		PLR	Temporal distortion
				physically	subjectively		
Chapter 3	1 (Sec. 3.2)	red & blue	○	△ ¹	○ ²	×	Yes
	2 (Sec. 3.3)		○	×	×	○	No
Chapter 4	1 (Sec. 4.2)	glare & halo	○	○	×	×	Yes
	2 (Sec. 4.3)		○	×	○ ³	N/A	No

○: intended match, △: consequencely controlled, ×: no control

¹ Closely physically equiluminant in mean, supported by Bayesian statistics.

² Based on the heterochromatic flicker photometry method (Wagner and Boynton, 1972)

³ Matched by a luminance adjustment task.

One particularly robust finding from the previous studies on temporal perception is that the occurrence of temporal illusions seem to be a result of the increased physical magnitude of the stimulus (“more-is-longer” account), suggested by conducting the temporal perception tasks with stimuli associated with different sensory inputs. In the series of experiments that we conducted, saturation (for red / blue stimuli), global contrast (for glare and halo stimuli), and global spatial frequency were controlled by the colorimetric adjustments and geometrical properties of the stimulus. This control was to ensure that temporal distortion is not a result of irrelevant physical properties of the stimuli, apart from the luminance (*e.g.*, Matthews and Meck, 2016; Wearden et al., 2014; Benton and Redfern, 2016; Wilms and Oberfeld, 2018; Bruno and Johnston, 2010; Aaen-Stockdale et al., 2011).

Although many previous findings have generally indicated temporal distortions between stimuli with different stimulus magnitude (see 2.1), temporal distortion did not occur in conditions where the physical luminance contradicts (Red & blue Exp.2, Glare & halo Exp.2). Another interesting finding is that temporal illusion was observed even when the subjective magnitude of the stimuli differed but was physically controlled (Glare & halo Exp.1). In particular, the perceived duration of the apparently brighter stimuli (glare stimuli) was shorter than that of the controlled stimuli (halo stimuli), in contrast with the

well-known “more-is-longer” account. These results suggest the possibility that temporal processing depends on the confluence of both the external magnitude and perceived subjective magnitude. In other words, temporal perception of visual stimuli is influenced by higher-level systems in visual processing and is not determined solely by the physical magnitude.

A further contribution of this study is the consideration of pupil response to the “magnitude effect” and temporal perception model. In this study (except Glare & halo Exp.2), pupillometry was adopted to the experiments for PLR matching purpose and to reveal how pupillary response is involved in temporal distortion. Table 5.2.1 shows that temporal distortion occurred when the PLR amplitude did not match within the stimulus condition, even though the physical or the subjective magnitude was matched (Red & blue Exp.1, Glare & halo Exp.1). Notably, the magnitude relationship matches among these results: the perceived duration of red and halo (smaller PLR) was judged longer than that of blue and glare (larger PLR), respectively. These findings demonstrate that the pupillary response somehow plays a role in temporal perception from a phenomenological perspective. One explanation to this relationship is the fluctuation in the amount of incident light entering the pupil, leading to the modulation of different degrees with regards to neural activation in visual-related regions. As previously mentioned in section 3.4 and section 4.4, the pupil area of the blue and glare stimuli was approximately only 30% of that for the red and halo stimuli. Since more significant pupillary constriction is known to result in lower EEG signals and responses of V1 (*e.g.*, Bombeke et al., 2016; Suzuki et al., 2019a), stimuli that induce a relatively smaller PLR may result in temporal overestimation by relatively larger neural activity in visual-related areas, based on the coding efficiency model (Eagleman and Pariyadath, 2009).

Here, we will discuss how the findings can impact further research in the field, through the stated research questions.

Research question 1: What is the potential effect of color (especially red v.s. blue) on temporal perception under careful stimuli control? Will different equiluminant methods result in different temporal illusions? If so, what is the causal mechanism?

The results of the study showed that the perceived duration of red was overestimated compared to blue, even when the physical aspects of the stimuli were strictly controlled in subjectively (\cong physically) equiluminant conditions. As previous studies have reported inconsistent findings (see 2.6.1), this study not just provides the fact that red was subjectively-longer but also should raises the importance of what equiluminant methods to use. In addition, the fact that PLR amplitude matching resulted in fading of the

temporal illusion should also provide a new perspective for future studies.

Research question 2: Is subjective magnitude itself sufficient to induce temporal illusions when the physical intensity is identical? In other words, does temporal processing depend on the confluence of both external magnitude and perceived subjective magnitude?

By utilizing visual illusions that modulate subjective brightness without the change in physical luminance, we found that temporal perception is also influenced by the illusory brightness. This could be an important finding as the results also mean that perceptual representations of the magnitude, which is assumed to link temporal perception, depends on the confluence of external stimulation and internal processing.

Research question 3: What is the relationship between pupillary response and temporal perception? Can pupil diameter be an index for subjective temporal perception? Or does pupil size affect temporal perception?

Although the physiological models suggesting a differential effect of different PLR amplitudes on temporal perception are currently lacking, this study's newly found causality between the PLR matching and temporal distortion effect can be explained by neural intensity fluctuations based on the amount of incident light entering the pupil. In the context of the coding efficiency model ([Eagleman and Pariyadath, 2009](#)), the pupil size seems to affect temporal perception and not vice-versa.

Here, we will note a few limitations in the study. First, we concluded that temporal perception can be influenced by higher-level systems in visual processing and is not determined solely by the physical magnitude. However, this does not imply that temporal perception only occurs at higher-order cognition in our visual system. On the contrary, our visual perception is achieved by a bidirectional interaction: sensory-based lower-level processing and a top-down process from higher-level cortices of the brain (*e.g.*, [Lamme and Roelfsema, 2000](#); [Hochstein and Ahissar, 2002](#)). As suggested by studies that support the “more-is-longer” account, temporal distortion can occur by a difference in physical magnitude, and therefore, it is possible that temporal perception relies on both low- and higher-order processing. Second, the mechanisms of temporal processing are known to vary between sub-second (milliseconds) and supra-second (seconds to minutes) interval ranges ([Näätänen et al., 2004](#); [Lewis and Miall, 2003](#)). Since this study's focus was on the judgment of intervals ranging from 1,600 ms-2,400 ms, not just the neural mechanisms but the implications of the PLR on temporal perception may differ in other temporal ranges. In fact, the pupil diameter is known to gradually dilate back to the baseline size after a certain

period of time from the PLR (*e.g.*, [Mathôt, 2018](#)). Additionally, recent studies have suggested that the PLR profile differs in late components, especially in response to blueish stimulus, as ipRGCs ([Markwell et al., 2010](#)) respond much slowly to light than other photoreceptors. Therefore, future studies should further confirm the relationship between pupillary response and temporal perception in other temporal ranges. Finally, although we suggested several results throughout this thesis, the relationship between the pupillary response and the temporal perception is based on phenomenology. Therefore, further considerations incorporating psychology, optical, and neuroscience approaches will be required to yield further discussions on theoretical frameworks and the probable mechanism, which should provide an important clue to elucidate the underlying mechanism of temporal perception in humans.

Publication List

List of Papers with Referee's Review

First-authored

- Yuya Kinzuka, Fumiaki Sato, Tetsuto Minami & Shigeki Nakauchi. “The effect of red/blue color stimuli on temporal perception under different pupillary responses induced by different equiluminant methods.” *Plos one*, 17(6), e0270110. 2022. <https://doi.org/10.1371/journal.pone.0270110>
- Yuya Kinzuka, Fumiaki Sato, Tetsuto Minami & Shigeki Nakauchi. “Effect of glare illusion - induced perceptual brightness on temporal perception.” *Psychophysiology*, 58(9), e13851, 2021. <https://doi.org/10.1111/psyp.13851>
- Yuya Kinzuka, Tetsuto Minami & Shigeki Nakauchi. “Pupil dilation reflects English /l//r/ discrimination ability for Japanese learners of English: a pilot study.” *Scientific Reports*, 10(1), 1-9, 2020. <https://doi.org/10.1038/s41598-020-65020-1>

List of Papers at International Conference with Referee's Review

First-authored

- Yuya Kinzuka, Fumiaki Sato, Tetsuto Minami & Shigeki Nakauchi. “Effect of Red/Blue on temporal perception and pupillary response by different equiluminant methods” *32nd International Congress of Psychology*, Czech Republic, July 19-24, 2020, Rescheduled to July 18-23, 2021.
- Yuya Kinzuka, Fumiaki Sato, Tetsuto Minami & Shigeki Nakauchi. “Association between temporal perception and pupillary response in Red/Blue stimuli” *Vision Sciences Society 2019 Annual Meeting*, Florida, U.S.A., May 17-22, 2019. *Journal of Vision (suppl.)*, 2019. <https://doi.org/10.1167/19.10.164a>

Bibliography

- [1] TIMES~, Wireless to THE NEW YORK (1929). Einstein Is Found Hiding On Birthday: Busy With Gift Microscope. *New York Times, Published on 1929 March 15th*, 3–3, 3, url: <https://www.nytimes.com/1929/03/15/archives/einstein-is-found-hiding-on-birthday-busy-with-gift-microscope-like.html>, accessed on 24th August 2021.
- [2] Einstein, Albert (1929/2011). *The ultimate quotable Einstein*: Princeton University Press
- [3] Muller, Timothy, & Nobre, Anna C (2014). Flow of time: perceiving the passage of time: neural possibilities. *Annals of the New York Academy of Sciences*, 1326(1), 60, doi: <https://doi.org/10.1111/nyas.12545>.
- [4] James, William, Burkhardt, Frederick, Bowers, Fredson, & Skrupskelis, Ignas K (1890). *The principles of psychology, I*: Macmillan London, doi: <https://doi.org/10.1037/10538-000>, doi: <https://doi.org/10.1037/10538-000>
- [5] Myers, Gerald E. (1971). William James on Time Perception. *Philosophy of Science*, 38(3), 353-360, doi: <https://doi.org/10.1086/288376>.
- [6] Grondin, Simon (2010). Timing and time perception: A review of recent behavioral and neuroscience findings and theoretical directions. *Attention, Perception, & Psychophysics*, 72(3), 561–582, doi: <https://doi.org/10.3758/APP.72.3.561>.
- [7] Matthews, William J, & Meck, Warren H (2016). Temporal cognition: Connecting subjective time to perception, attention, and memory.. *Psychological bulletin*, 142(8), 865, doi: <https://doi.org/10.1037/bul0000045>.
- [8] Grimes, William N, Songco-Aguas, Adree, & Rieke, Fred (2018). Parallel processing of rod and cone signals: retinal function and human perception. *Annual Review of Vision Science*, 4, 123–141, doi: <https://doi.org/10.1146/annurev-vision-091517-034055>.
- [9] Rushton, WAH (1972). Review lecture. Pigments and signals in colour vision. *The Journal of physiology*, 220(3), 1P, doi: <https://doi.org/10.1113/jphysiol.1972.sp009719>.
- [10] Eagleman, David M (2008). Human time perception and its illusions. *Current opinion in neuro-*

- biology*, 18(2), 131–136, doi: <https://doi.org/10.1016/j.conb.2008.06.002>.
- [11] Rammsayer, Thomas H, & Verner, Martin (2014). The effect of nontemporal stimulus size on perceived duration as assessed by the method of reproduction. *Journal of Vision*, 14(5), 17–17, doi: <https://doi.org/10.1167/14.5.17>.
 - [12] Walsh, Vincent (2003). A theory of magnitude: common cortical metrics of time, space and quantity. *Trends in cognitive sciences*, 7(11), 483–488, doi: <https://doi.org/10.1016/j.tics.2003.09.002>.
 - [13] Smets, Gerda (1969). Time expression of red and blue. *Perceptual and Motor Skills*, 29(2), 511–514, doi: <https://doi.org/10.2466/pms.1969.29.2.511>.
 - [14] Goldstone, Sanford, & Goldfarb, Joyce Levis (1964). Auditory and visual time judgment. *The Journal of General Psychology*, 70(2), 369–387, doi: <https://doi.org/10.1080/00221309.1964.9920609>.
 - [15] Goldstone, Sanford, Lhamon, William T, & Sechzer, Jeri (1978). Light intensity and judged duration. *Bulletin of the Psychonomic Society*, 12(1), 83–84, doi: <https://doi.org/10.3758/BF03329633>.
 - [16] Shibasaki, Masahiro, & Masataka, Nobuo (2014). The color red distorts time perception for men, but not for women. *Scientific reports*, 4, 5899, doi: <https://doi.org/10.1038/srep05899>.
 - [17] Thönes, S, Von Castell, C, Ifflinger, J, & Oberfeld, D (2018). Color and time perception: Evidence for temporal overestimation of blue stimuli. *Scientific reports*, 8(1), 1688, doi: <https://doi.org/10.1038/s41598-018-19892-z>.
 - [18] Brigner, Willard L (1986). Effect of perceived brightness on perceived time. *Perceptual and motor skills*, 63(2), 427–430, doi: <https://doi.org/10.2466/pms.1986.63.2.427>.
 - [19] Casini, Laurence, & Macar, Françoise (1997). Effects of attention manipulation on judgments of duration and of intensity in the visual modality. *Memory & cognition*, 25(6), 812–818, doi: <https://doi.org/10.3758/BF03211325>.
 - [20] Gorn, Gerald J, Chattopadhyay, Amitava, Sengupta, Jaideep, & Tripathi, Shashank (2004). Waiting for the web: how screen color affects time perception. *Journal of marketing research*, 41(2), 215–225, doi: <https://doi.org/10.1509/jmkr.41.2.215.2866>.
 - [21] Szabadi, Elemer (2012). Modulation of physiological reflexes by pain: role of the locus coeruleus. *Frontiers in integrative neuroscience*, 6, 94, doi: <https://doi.org/10.3389/fnint.2012.00094>.

- [22] Janisse, Michel Pierre (1977). *Pupillometry: The psychology of the pupillary response*: Hemisphere Pub
- [23] Wardhani, Intan K, Boehler, C Nico, & Mathot, Sebastiaan (2022). The influence of pupil responses on subjective brightness perception. *Perception*, 03010066221094757, doi: <https://doi.org/10.1177/0301006622109475>.
- [24] Markwell, Emma L, Feigl, Beatrix, & Zele, Andrew J (2010). Intrinsically photosensitive melanopsin retinal ganglion cell contributions to the pupillary light reflex and circadian rhythm. *Clinical and Experimental Optometry*, 93(3), 137–149, doi: <https://doi.org/10.1111/j.1444-0938.2010.00479.x>.
- [25] Mathôt, Sebastiaan (2018). Pupillometry: Psychology, physiology, and function. *Journal of Cognition*, 1(1), doi: <https://doi.org/10.5334/joc.18>.
- [26] Herbst, Kristina, Sander, Birgit, Milea, Dan, Lund-Andersen, Henrik, & Kawasaki, Aki (2011). Test–retest repeatability of the pupil light response to blue and red light stimuli in normal human eyes using a novel pupillometer. *Frontiers in Neurology*, 2, 10, doi: <https://doi.org/10.3389/fneur.2011.00010>.
- [27] Young, Rockefeller SL, & Kimura, Eiji (2008). Pupillary correlates of light-evoked melanopsin activity in humans. *Vision research*, 48(7), 862–871, doi: <https://doi.org/10.1016/j.visionres.2007.12.016>.
- [28] Arstila, Valtteri, & Lloyd, Dan (2014). *Subjective time: The philosophy, psychology, and neuroscience of temporality*: Mit Press
- [29] Pande, Babita, & Pati, Atanu Kumar (2010). Overestimation/underestimation of time: concept confusion hoodwink conclusion. *Biological rhythm research*, 41(5), 379–390, doi: <https://doi.org/10.1080/09291010903299111>.
- [30] Hoagland, Hudson (1933). The physiological control of judgments of duration: Evidence for a chemical clock. *The Journal of General Psychology*, 9(2), 267–287, doi: <https://doi.org/10.1080/00221309.1933.9920937>.
- [31] Gil, Sandrine, & Droit-Volet, Sylvie (2011). “Time flies in the presence of angry faces”... depending on the temporal task used!. *Acta psychologica*, 136(3), 354–362, doi: <https://doi.org/10.1016/j.actpsy.2010.12.010>.
- [32] Xuan, Bin, Zhang, Daren, He, Sheng, & Chen, Xiangchuan (2007). Larger stimuli are judged to last longer. *Journal of vision*, 7(10), 2–2, doi: <https://doi.org/10.1167/7.10.2>.

- [33] Kanai, Ryota, Paffen, Chris LE, Hogendoorn, Hinze, & Verstraten, Frans AJ (2006). Time dilation in dynamic visual display. *Journal of vision*, 6(12), 8–8, doi: <https://doi.org/10.1167/6.12.8>.
- [34] Matthews, William J, Stewart, Neil, & Wearden, John H (2011). Stimulus intensity and the perception of duration.. *Journal of Experimental Psychology: Human perception and performance*, 37(1), 303, doi: <https://doi.org/10.1037/a0019961>.
- [35] Jones, Luke A, Poliakoff, Ellen, & Wells, Jill (2009). Good vibrations: Human interval timing in the vibrotactile modality. *The Quarterly Journal of Experimental Psychology*, 62(11), 2171–2186, doi: <https://doi.org/10.1080/17470210902782200>.
- [36] Lang, Peter J (2005). International affective picture system (IAPS): Affective ratings of pictures and instruction manual. *Technical report*, doi: https://doi.org/10.1007/978-3-319-28099-8_42-1.
- [37] Angrilli, Alessandro, Cherubini, Paolo, Pavese, Antonella, & Manfredini, Sara (1997). The influence of affective factors on time perception. *Perception & psychophysics*, 59(6), 972–982, doi: <https://doi.org/10.3758/BF03205512>.
- [38] Bradley, Margaret, & Lang, Peter J (1999). *The International affective digitized sounds (IADS)[: stimuli, instruction manual and affective ratings*: NIMH Center for the Study of Emotion and Attention
- [39] Noulhiane, Marion, Mella, Nathalie, Samson, S, Ragot, R, & Pouthas, Viviane (2007). How emotional auditory stimuli modulate time perception.. *Emotion*, 7(4), 697, doi: <https://doi.org/10.1037/1528-3542.7.4.697>.
- [40] Droit-Volet, Sylvie, Brunot, Sophie, & Niedenthal, Paula (2004). BRIEF REPORT Perception of the duration of emotional events. *Cognition and Emotion*, 18(6), 849–858, doi: <https://doi.org/10.1080/02699930341000194>.
- [41] Treisman, Michel (1963). Temporal discrimination and the indifference interval: Implications for a model of the" internal clock".. *Psychological Monographs: General and Applied*, 77(13), 1, doi: <https://doi.org/10.1037/h0093864>.
- [42] Gibbon, John, Church, Russell M, Meck, Warren H et al. (1984). Scalar timing in memory. *Annals of the New York Academy of sciences*, 423(1), 52–77, doi: <https://doi.org/10.1111/j.1749-6632.1984.tb23417.x>.
- [43] Wearden, John, O'Donoghue, Alan, Ogden, Ruth, & Montgomery, Catharine (2014). Subjective Duration in the Laboratory and the World Outside. *Subjective time: The philosophy, psychology,*

- and neuroscience of temporality, 287, doi: <https://doi.org/10.7551/mitpress/8516.001.0001>.
- [44] Buetti, Domenica, & Walsh, Vincent (2009). The parietal cortex and the representation of time, space, number and other magnitudes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1525), 1831–1840, doi: <https://doi.org/10.1098/rstb.2009.0028>.
- [45] Gibbon, John (1977). Scalar expectancy theory and Weber's law in animal timing.. *Psychological review*, 84(3), 279, doi: <https://doi.org/10.1037/0033-295X.84.3.279>.
- [46] Wearden, John H, & Lejeune, Helga (2008). Scalar properties in human timing: Conformity and violations. *The Quarterly Journal of Experimental Psychology*, 61(4), 569–587, doi: <https://doi.org/10.1080/17470210701282576>.
- [47] Baudouin, Alexia, Vanneste, Sandrine, Isingrini, Michel, & Pouthas, Viviane (2006). Differential involvement of internal clock and working memory in the production and reproduction of duration: A study on older adults. *Acta Psychologica*, 121(3), 285–296, doi: <https://doi.org/10.1016/j.actpsy.2005.07.004>.
- [48] Church, Russell M, & Deluty, Marvin Z (1977). Bisection of temporal intervals.. *Journal of Experimental Psychology: Animal Behavior Processes*, 3(3), 216, doi: <https://doi.org/10.1037/0097-7403.3.3.216>.
- [49] Allan, Lorraine G, & Kristofferson, Alfred B (1974). Psychophysical theories of duration discrimination. *Perception & Psychophysics*, 16(1), 26–34, doi: <https://doi.org/10.3758/BF03203244>.
- [50] Desiderato, Otello (1964). Effect of anxiety and stress on reaction time and temporal generalization. *Psychological Reports*, 14(1), 51–58, doi: <https://doi.org/10.2466/pr0.1964.14.1.51>.
- [51] Meck, Warren H (1996). Neuropharmacology of timing and time perception. *Cognitive brain research*, 3(3-4), 227–242, doi: [https://doi.org/10.1016/0926-6410\(96\)00009-2](https://doi.org/10.1016/0926-6410(96)00009-2).
- [52] Wichmann, Felix A, & Hill, N Jeremy (2001). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & psychophysics*, 63(8), 1293–1313, doi: <https://doi.org/10.3758/BF03194544>.
- [53] Eagleman, David M, & Pariyadath, Vani (2009). Is subjective duration a signature of coding efficiency? *Philosophical transactions of the royal society B: Biological sciences*, 364(1525), 1841–1851, doi: <https://doi.org/10.1098/rstb.2009.0026>.

- [54] Noguchi, Yasuki, & Kakigi, Ryusuke (2006). Time representations can be made from non-temporal information in the brain: an MEG study. *Cerebral Cortex*, 16(12), 1797–1808, doi: <https://doi.org/10.1093/cercor/bhj117>.
- [55] LeDoux, Joseph (1998). *The emotional brain: The mysterious underpinnings of emotional life*: Simon and Schuster
- [56] Babin, Barry J, Hardesty, David M, & Suter, Tracy A (2003). Color and shopping intentions: The intervening effect of price fairness and perceived affect. *Journal of business research*, 56(7), 541–551, doi: [https://doi.org/10.1016/S0148-2963\(01\)00246-6](https://doi.org/10.1016/S0148-2963(01)00246-6).
- [57] Kwallek, Nancy, Lewis, Carol M, & Robbins, Ann S (1988). Effects of office interior color on workers' mood and productivity. *Perceptual and Motor Skills*, 66(1), 123–128, doi: <https://doi.org/10.2466/pms.1988.66.1.123>.
- [58] Hill, Russell A, & Barton, Robert A (2005). Psychology: red enhances human performance in contests. *Nature*, 435(7040), 293, doi: <https://doi.org/10.1038/435293a>.
- [59] Pomerleau, Vincent Jetté, Fortier-Gauthier, Ulysse, Corriveau, Isabelle, Dell'Acqua, Roberto, & Jolicœur, Pierre (2014). Colour-specific differences in attentional deployment for equiluminant pop-out colours: evidence from lateralised potentials. *International Journal of Psychophysiology*, 91(3), 194–205, doi: <https://doi.org/10.1016/j.ijpsycho.2013.10.016>.
- [60] Buechner, Vanessa L, Maier, Markus A, Lichtenfeld, Stephanie, & Schwarz, Sascha (2014). Red-take a closer look. *PLoS One*, 9(9), e108111, doi: <https://doi.org/10.1371/journal.pone.0108111>.
- [61] Tchernikov, Illia, & Fallah, Mazyar (2010). A color hierarchy for automatic target selection. *PLoS One*, 5(2), e9338, doi: <https://doi.org/10.1371/journal.pone.0009338>.
- [62] Ali, MR (1972). Pattern of EEG recovery under photic stimulation by light of different colors. *Electroencephalography and Clinical Neurophysiology*, 33(3), 332–335, doi: [https://doi.org/10.1016/0013-4694\(72\)90162-9](https://doi.org/10.1016/0013-4694(72)90162-9).
- [63] Jacobs, Keith W, & Hustmyer Jr, Frank E (1974). Effects of four psychological primary colors on GSR, heart rate and respiration rate. *Perceptual and motor skills*, 38(3), 763–766, doi: <https://doi.org/10.2466/pms.1974.38.3.763>.
- [64] Elliot, Andrew J, Payen, Vincent, Brisswalter, Jeanick, Cury, Francois, & Thayer, Julian F (2011). A subtle threat cue, heart rate variability, and cognitive performance. *Psychophysiology*, 48(10), 1340–1345, doi: <https://doi.org/10.1111/j.1469-8986.2011.01216.x>.

-
- [65] Mehta, Ravi, & Zhu, Rui Juliet (2009). Blue or red? Exploring the effect of color on cognitive task performances. *Science*, 323(5918), 1226–1229, doi: <https://doi.org/10.1126/science.1169144>.
- [66] Elliot, Andrew J, & Aarts, Henk (2011). Perception of the color red enhances the force and velocity of motor output.. *Emotion*, 11(2), 445, doi: <https://doi.org/10.1037/a0022599>.
- [67] Xia, Tiansheng, Song, Lu, Wang, Ting T, Tan, Ling, & Mo, Lei (2016). Exploring the effect of red and blue on cognitive task performances. *Frontiers in psychology*, 7, 784, doi: <https://doi.org/10.3389/fpsyg.2016.00784>.
- [68] Soldat, Alexander S, Sinclair, Robert C, & Mark, Melvin M (1997). Color as an environmental processing cue: External affective cues can directly affect processing strategy without affecting mood. *Social cognition*, 15(1), 55–71, doi: <https://doi.org/10.1521/soco.1997.15.1.55>.
- [69] Elliot, Andrew J, Maier, Markus A, Moller, Arlen C, Friedman, Ron, & Meinhardt, Jörg (2007). Color and psychological functioning: The effect of red on performance attainment.. *Journal of experimental psychology: General*, 136(1), 154, doi: <https://doi.org/10.1037/0096-3445.136.1.154>.
- [70] Kinzuka, Yuya, Sato, Fumiaki, Minami, Tetsuto, & Nakauchi, Shigeki (2022). The effect of red/blue color stimuli on temporal perception under different pupillary responses induced by different equiluminant methods. *Plos one*, 17(6), e0270110, doi: <https://doi.org/10.1371/journal.pone.0270110>.
- [71] Caldwell, John A, & Jones, Gary E (1985). The effects of exposure to red and blue light on physiological indices and time estimation. *Perception*, 14(1), 19–29, doi: <https://doi.org/10.1068/p140019>.
- [72] Katsuura, Tetsuo, Yasuda, Takumi, Shimomura, Yoshihiro, & Iwanaga, Koichi (2007). Effects of monochromatic light on time sense for short intervals. *Journal of physiological anthropology*, 26(2), 95–100, doi: <https://doi.org/10.2114/jpa2.26.95>.
- [73] Yang, Pei-Ling, Tsujimura, Sei-ichi, Matsumoto, Akiko, Yamashita, Wakayo, & Yeh, Su-Ling (2018). Subjective time expansion with increased stimulation of intrinsically photosensitive retinal ganglion cells. *Scientific reports*, 8(1), 11693, doi: <https://doi.org/10.1038/s41598-018-29613-1>.
- [74] Walters, Jean, Apter, Michael J, & Svebak, Sven (1982). Color preference, arousal, and the theory of psychological reversals. *Motivation and emotion*, 6(3), 193–215, doi: <https://doi.org/10.1007/BF01531851>.
-

- [org/10.1007/BF00992245](https://doi.org/10.1007/BF00992245).
- [75] Long, Gerald M, & Beaton, Robert J (1980). The contribution of visual persistence to the perceived duration of brief targets. *Perception & Psychophysics*, 28(5), 422–430, doi: <https://doi.org/10.3758/bf03204886>.
 - [76] Mathôt, Sebastiaan (2020). Tuning the senses: How the pupil shapes vision at the earliest stage. *Annual Review of Vision Science*, 6(1), 433–451, doi: <https://doi.org/10.1146/annurev-vision-030320-062352>.
 - [77] Ellis, CJ (1981). The pupillary light reflex in normal subjects.. *British Journal of Ophthalmology*, 65(11), 754–759, doi: <https://doi.org/10.1136/bjo.65.11.754>.
 - [78] Mathôt, Sebastiaan, Van der Linden, Lotje, Grainger, Jonathan, & Vitu, Françoise (2013). The pupillary light response reveals the focus of covert visual attention. *PLoS One*, 8(10), doi: <https://doi.org/10.1371/journal.pone.0078168>.
 - [79] Ostrin, Lisa A (2018). The ipRGC-driven pupil response with light exposure and refractive error in children. *Ophthalmic and Physiological Optics*, 38(5), 503–515, doi: <https://doi.org/10.1111/opo.12583>.
 - [80] Gamlin, PD, & Clarke, Robert J (1995). The pupillary light reflex pathway of the primate.. *Journal of the American Optometric Association*, 66(7), 415–418.
 - [81] Gamlin, Paul DR, McDougal, David H, Pokorny, Joel, Smith, Vivianne C, Yau, King-Wai, & Dacey, Dennis M (2007). Human and macaque pupil responses driven by melanopsin-containing retinal ganglion cells. *Vision research*, 47(7), 946–954, doi: <https://doi.org/10.1016/j.visres.2006.12.015>.
 - [82] Chougule, Pratik S, Najjar, Raymond P, Finkelstein, Maxwell T, Kandiah, Nagaendran, & Milea, Dan (2019). Light-Induced Pupillary Responses in Alzheimer’s Disease. *Frontiers in Neurology*, 10, doi: <https://doi.org/10.3389/fneur.2019.00360>.
 - [83] Bradley, Margaret M, Miccoli, Laura, Escrig, Miguel A, & Lang, Peter J (2008). The pupil as a measure of emotional arousal and autonomic activation. *Psychophysiology*, 45(4), 602–607, doi: <https://doi.org/10.1111/j.1469-8986.2008.00654.x>.
 - [84] Einhäuser, Wolfgang, Stout, James, Koch, Christof, & Carter, Olivia (2008). Pupil dilation reflects perceptual selection and predicts subsequent stability in perceptual rivalry. *Proceedings of the National Academy of Sciences*, 105(5), 1704–1709, doi: <https://doi.org/10.1073/pnas.0707727105>.

-
- [85] Aston-Jones, Gary, & Cohen, Jonathan D (2005). An integrative theory of locus coeruleus-norepinephrine function: adaptive gain and optimal performance. *Annu. Rev. Neurosci.*, 28, 403–450, doi: <https://doi.org/10.1146/annurev.neuro.28.061604.135709>.
- [86] Murphy, Peter R, O’Connell, Redmond G, O’Sullivan, Michael, Robertson, Ian H, & Balsters, Joshua H (2014). Pupil diameter covaries with BOLD activity in human locus coeruleus. *Human brain mapping*, 35(8), 4140–4154, doi: <https://doi.org/10.1002/hbm.22466>.
- [87] Kang, Olivia E, Huffer, Katherine E, & Wheatley, Thalia P (2014). Pupil dilation dynamics track attention to high-level information. *PLoS One*, 9(8), e102463, doi: <https://doi.org/10.1371/journal.pone.0102463>.
- [88] Peinkhofer, Costanza, Knudsen, Gitte M, Moretti, Rita, & Kondziella, Daniel (2019). Cortical modulation of pupillary function: systematic review. *PeerJ*, 7, e6882, doi: <https://doi.org/10.7717/peerj.6882>.
- [89] Faber, Nathaniel J (2017). Neuromodulation of pupil diameter and temporal perception. *The Journal of Neuroscience*, 37(11), 2806, doi: <https://doi.org/10.1523/jneurosci.0012-17.2017>.
- [90] Suzuki, Tomoki W, Kunimatsu, Jun, & Tanaka, Masaki (2016). Correlation between pupil size and subjective passage of time in non-human primates. *Journal of Neuroscience*, 36(44), 11331–11337, doi: <https://doi.org/10.1523/JNEUROSCI.2533-16.2016>.
- [91] Kruijne, Wouter, Olivers, Christian NL, & van Rijn, Hedderik (2021). Neural repetition suppression modulates time perception: Evidence from electrophysiology and pupillometry. *Journal of cognitive neuroscience*, 33(7), 1230–1252, doi: https://doi.org/10.1162/jocn_a_01705.
- [92] Henson, Richard NA (2003). Neuroimaging studies of priming. *Progress in neurobiology*, 70(1), 53–81, doi: [https://doi.org/10.1016/S0301-0082\(03\)00086-8](https://doi.org/10.1016/S0301-0082(03)00086-8).
- [93] Suzuki, Tomoki W, & Tanaka, Masaki (2017). Causal role of noradrenaline in the timing of internally generated saccades in monkeys. *Neuroscience*, 366, 15–22, doi: <https://doi.org/10.1016/j.neuroscience.2017.10.003>.
- [94] Toscano-Zapién, Anna L, Velázquez-López, Daniel, & Velázquez-Martínez, David N (2016). Attentional mechanisms during the performance of a subsecond timing task. *Plos one*, 11(7), e0158508, doi: <https://doi.org/10.1371/journal.pone.0158508>.
- [95] Laeng, Bruno, Sirois, Sylvain, & Gredebäck, Gustaf (2012). Pupillometry: A window to the preconscious? *Perspectives on psychological science*, 7(1), 18–27, doi: <https://doi.org/10.1177/1745691611427305>.
-

- [96] Joshi, Siddhartha, & Gold, Joshua I (2020). Pupil size as a window on neural substrates of cognition. *Trends in cognitive sciences*, 24(6), 466–480, doi: <https://doi.org/10.1016/j.tics.2020.03.005>.
- [97] Robinson, Sophie (2011). Do You See What I See? (TV Program). Aug, url: <https://www.bbc.co.uk/programmes/b013c8tb>, accessed on 7th October 2022.
- [98] Kinzuka, Yuya, Sato, Fumiaki, Minami, Tetsuto, & Nakauchi, Shigeki (2021). Effect of glare illusion-induced perceptual brightness on temporal perception. *Psychophysiology*, 58(9), e13851, doi: <https://doi.org/10.1111/psyp.13851>.
- [99] Brainard, David H (1997). The psychophysics toolbox. *Spatial vision*, 10(4), 433–436, doi: <https://doi.org/10.1163/156856897x00357>.
- [100] Pelli, Denis G (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial vision*, 10(4), 437–442, doi: <https://doi.org/10.1163/156856897x00366>.
- [101] Kleiner, Mario, Brainard, David, & Pelli, Denis (2007). What’s new in Psychtoolbox-3? *Perception*, doi: <https://doi.org/10.1068/v070821>.
- [102] Bone, Richard A, & Landrum, John T (2004). Heterochromatic flicker photometry. *Archives of biochemistry and biophysics*, 430(2), 137–142, doi: <https://doi.org/10.1016/j.abb.2004.04.003>.
- [103] Wagner, Gunther, & Boynton, Robert M (1972). Comparison of four methods of heterochromatic photometry. *JOSA*, 62(12), 1508–1515, doi: <https://doi.org/10.1364/JOSA.62.001508>.
- [104] Pokorny, Joel, Smith, Vivianne C, & Lutze, Margaret (1989). Heterochromatic modulation photometry. *JOSA A*, 6(10), 1618–1623, doi: <https://doi.org/10.1364/JOSAA.6.001618>.
- [105] Grondin, Simon, Ouellet, Bastien, & Roussel, Marie-Eve (2004). Benefits and limits of explicit counting for discriminating temporal intervals.. *Canadian Journal of Experimental Psychology/Revue canadienne de psychologie expérimentale*, 58(1), 1, doi: <https://doi.org/10.1037/h0087436>.
- [106] Mathôt, Sebastiaan et al. (2013). A simple way to reconstruct pupil size during eye blinks. <https://doi.org/10.6084/m9.figshare.688002>, doi: <https://doi.org/10.6084/m9.figshare.688002>.
- [107] Prins, Nicolaas, & Kingdom, Frederick AA (2018). Applying the model-comparison approach to test specific research hypotheses in psychophysical research using the Palamedes toolbox.

- Frontiers in psychology*, 9, 1250, doi: <https://doi.org/10.3389/fpsyg.2018.01250>.
- [108] Seaman, Michael A, Levin, Joel R, & Serlin, Ronald C (1991). New developments in pairwise multiple comparisons: some powerful and practicable procedures.. *Psychological Bulletin*, 110(3), 577, doi: <https://doi.org/10.1037/0033-2909.110.3.577>.
- [109] JASP Team (2020). JASP (Version 0.14.1)[Computer software]. url: <https://jasp-stats.org/>.
- [110] Ortega, Alonso, & Navarrete, Gorka (2017). Bayesian Hypothesis Testing: An Alternative to Null Hypothesis Significance Testing (NHST) in Psychology and Social Sciences. In *Bayesian inference()*: IntechOpen, doi: <https://doi.org/10.5772/intechopen.70230>
- [111] Bombeke, Klaas, Duthoo, Wout, Mueller, Sven C, Hopf, Jens-Max, & Boehler, C Nico (2016). Pupil size directly modulates the feedforward response in human primary visual cortex independently of attention. *NeuroImage*, 127, 67–73, doi: <https://doi.org/10.1016/j.neuroimage.2015.11.072>.
- [112] Suzuki, Yuta, Minami, Tetsuto, & Nakauchi, Shigeki (2019a). Pupil Constriction in the Glare Illusion Modulates the Steady-State Visual Evoked Potentials. *Neuroscience*, 416, 221–228, doi: <https://doi.org/10.1016/j.neuroscience.2019.08.003>.
- [113] Mathôt, Sebastiaan, Fabius, Jasper, Van Heusden, Elle, & Van der Stigchel, Stefan (2018). Safe and sensible preprocessing and baseline correction of pupil-size data. *Behavior research methods*, 50(1), 94–106, doi: <https://doi.org/10.3758/s13428-017-1007-2>.
- [114] Watson, Andrew B, & Yellott, John I (2012). A unified formula for light-adapted pupil size. *Journal of vision*, 12(10), 12–12, doi: <https://doi.org/10.1167/12.10.12>.
- [115] Wang, Chin-An, & Munoz, Douglas P (2015). A circuit for pupil orienting responses: implications for cognitive modulation of pupil size. *Current opinion in neurobiology*, 33, 134–140, doi: <https://doi.org/10.1016/j.conb.2015.03.018>.
- [116] Tabachnick, Barbara G, & Fidell, Linda S (2007). *Using multivariate statistics*, 5: Pearson
- [117] Dienes, Zoltan (2014). Using Bayes to get the most out of non-significant results. *Frontiers in psychology*, 5, 781, doi: <https://doi.org/10.3389/fpsyg.2014.00781>.
- [118] Laeng, Bruno, & Endestad, Tor (2012). Bright illusions reduce the eye's pupil. *Proceedings of the National Academy of Sciences*, 109(6), 2162–2167, doi: <https://doi.org/10.1073/pnas.1118298109>.
- [119] Sandoval Salinas, Claudia, Hermans, Stijn, Sandoval, José, Smet, Kevin AG, Hanselaer, Peter,

- & Colombo, Elisa (2020). Relationship between pupillary size, brightness, and photoreceptor responses for unrelated self-luminous stimuli at low photopic light levels. *Color Research & Application*, 45(6), 977–991, doi: <https://doi.org/10.1002/col.22546>.
- [120] Binda, Paola, Pereverzeva, Maria, & Murray, Scott O (2013). Pupil constrictions to photographs of the sun. *Journal of Vision*, 13(6), 8–8, doi: <https://doi.org/10.1167/13.6.8>.
- [121] Zavagno, Daniele, Tommasi, Luca, & Laeng, Bruno (2017). The eye pupil's response to static and dynamic illusions of luminosity and darkness. *i-Perception*, 8(4), 2041669517717754, doi: <https://doi.org/10.1177/2041669517717754>.
- [122] Suzuki, Yuta, Minami, Tetsuto, Laeng, Bruno, & Nakauchi, Shigeki (2019b). Colorful glares: Effects of colors on brightness illusions measured with pupillometry. *Acta psychologica*, 198, 102882, doi: <https://doi.org/10.1016/j.actpsy.2019.102882>.
- [123] Näätänen, Risto, Syssoeva, Olga, & Takegata, Rika (2004). Automatic time perception in the human brain for intervals ranging from milliseconds to seconds. *Psychophysiology*, 41(4), 660–663, doi: <https://doi.org/10.1111/j.1469-8986.2004.00182.x>.
- [124] Lewis, Penny A, & Miall, R Chris (2003). Brain activation patterns during measurement of sub-and supra-second intervals. *Neuropsychologia*, 41(12), 1583–1592, doi: [https://doi.org/10.1016/s0028-3932\(03\)00118-0](https://doi.org/10.1016/s0028-3932(03)00118-0).
- [125] Makin, Alexis DJ, Poliakoff, Ellen, Dillon, Joe, Perrin, Aimee, Mullet, Thomas, & Jones, Luke A (2012). The interaction between duration, velocity and repetitive auditory stimulation. *Acta psychologica*, 139(3), 524–531, doi: <https://doi.org/10.1016/j.actpsy.2012.01.013>.
- [126] Benton, Christopher P, & Redfern, Annabelle S (2016). Perceived duration increases with contrast, but only a little. *Frontiers in psychology*, 7, 1950, doi: <https://doi.org/10.3389/fpsyg.2016.01950>.
- [127] Vicario, Carmelo Mario (2011). Perceiving numbers affects the subjective temporal midpoint. *Perception*, 40(1), 23–29, doi: <https://doi.org/10.1068/p6800>.
- [128] Sasaki, Kyoshiro, & Yamada, Yuki (2017). Regular is longer. *I-perception*, 8(5), doi: <https://doi.org/10.1177/2041669517728944>.
- [129] Herbst, Sophie K, Javadi, Amir Homayoun, van der Meer, Elke, & Busch, Niko A (2013). How long depends on how fast—perceived flicker dilates subjective duration. *PloS one*, 8(10), e76074, doi: <https://doi.org/10.1371/journal.pone.0076074>.
- [130] Williams, Emily A, Yüksel, Ezgi M, Stewart, Andrew J, & Jones, Luke A (2019). Modality

- differences in timing and the filled-duration illusion: Testing the pacemaker rate explanation. *Attention, Perception, & Psychophysics*, 81(3), 823–845, doi: <https://doi.org/10.3758/s13414-018-1630-8>.
- [131] Gomez, Louis M, & Robertson, Lynn C (1979). The filled-duration illusion: The function of temporal and nontemporal set. *Perception & Psychophysics*, 25(5), 432–438, doi: <https://doi.org/10.3758/bf03199853>.
- [132] Block, Richard A, & Gruber, Ronald P (2014). Time perception, attention, and memory: a selective review. *Acta psychologica*, 149, 129–133, doi: <https://doi.org/10.1016/j.actpsy.2013.11.003>.
- [133] Titchener, Edward Bradford (1901). Experimental psychology: A manual of laboratory practice, Vol 1: Qualitative experiments: Part II. Instructor's manual..
- [134] Burton, Gregory (2001). The tenacity of historical misinformation: Titchener did not invent the Titchener illusion.. *History of Psychology*, 4(3), 228, doi: <https://doi.org/10.1037/1093-4510.4.3.228>.
- [135] Ono, Fuminori, & Kawahara, Jun-Ichiro (2007). The subjective size of visual stimuli affects the perceived duration of their presentation. *Perception & psychophysics*, 69(6), 952–957, doi: <https://doi.org/10.3758/bf03193932>.
- [136] Zavagno, Daniele, & Caputo, Giovanni (2001). The glare effect and the perception of luminosity. *Perception*, 30(2), 209–222, doi: <https://doi.org/10.1068/p3009>.
- [137] Zavagno, Daniele (1999). Some new luminance-gradient effects. *Perception*, 28(7), 835–838, doi: <https://doi.org/10.1068/p2633>.
- [138] Agostini, Tiziano, & Galmonte, Alessandra (2002). A new effect of luminance gradient on achromatic simultaneous contrast. *Psychonomic Bulletin & Review*, 9(2), 264–269, doi: <https://doi.org/10.3758/bf03196281>.
- [139] Tamura, Hideki, Nakauchi, Shigeki, & Koida, Kowa (2016). Robust brightness enhancement across a luminance range of the glare illusion. *Journal of vision*, 16(1), 10–10, doi: <https://doi.org/10.1167/16.1.10>.
- [140] Laeng, Bruno, Færevag, Fredrik Svardal, Tanggaard, Stine, & von Tetzchner, Stephen (2018). Pupillary responses to illusions of brightness in autism spectrum disorder. *i-Perception*, 9(3), 2041669518771716, doi: <https://doi.org/10.1177/2041669518771716>.
- [141] Morrone, M Concetta, Ross, John, & Burr, David (2005). Saccadic eye movements cause

- p>compression of time as well as space.
- Nature neuroscience*
- , 8(7), 950–954, doi:
- <https://doi.org/10.1038/nn1488>
- .
- [142] Engbert, Ralf, & Kliegl, Reinhold (2003). Microsaccades uncover the orientation of covert attention. *Vision research*, 43(9), 1035–1045, doi: [https://doi.org/10.1016/s0042-6989\(03\)00084-1](https://doi.org/10.1016/s0042-6989(03)00084-1).
- [143] JASP Team (2019). JASP (Version 0.11.1)[Computer software]. url: <https://jasp-stats.org/>.
- [144] Sulutvedt, Unni, Zavagno, Daniele, Lubell, Jamie, Leknes, Siri, Sigrid, A, & Laeng, Bruno (2021). Brightness perception changes related to pupil size. *Vision Research*, 178, 41–47, doi: <https://doi.org/10.1016/j.visres.2020.09.004>.
- [145] Murray, Scott O, Boyaci, Huseyin, & Kersten, Daniel (2006). The representation of perceived angular size in human primary visual cortex. *Nature neuroscience*, 9(3), 429–434, doi: <https://doi.org/10.1038/nn1641>.
- [146] Di Lollo, Vincent, Enns, James T, & Rensink, Ronald A (2000). Competition for consciousness among visual events: the psychophysics of reentrant visual processes.. *Journal of Experimental Psychology: General*, 129(4), 481, doi: <https://doi.org/10.1037/0096-3445.129.4.481>.
- [147] Grondin, Simon, Laflamme, Vincent, & Gontier, Émilie (2014). Effect on perceived duration and sensitivity to time when observing disgusted faces and disgusting mutilation pictures. *Attention, Perception, & Psychophysics*, 76(6), 1522–1534, doi: <https://doi.org/10.3758/s13414-014-0682-7>.
- [148] Lee, Kwang-Hyuk, Bhaker, Rajinder S, Mysore, Ashok, Parks, Randolph W, Birkett, Paul BL, & Woodruff, Peter WR (2009). Time perception and its neuropsychological correlates in patients with schizophrenia and in healthy volunteers. *Psychiatry Research*, 166(2-3), 174–183, doi: <https://doi.org/10.1016/j.psychres.2008.03.004>.
- [149] Wilms, Lisa, & Oberfeld, Daniel (2018). Color and emotion: effects of hue, saturation, and brightness. *Psychological research*, 82(5), 896–914, doi: <https://doi.org/10.1007/s00426-017-0880-8>.
- [150] Bruno, Aurelio, & Johnston, Alan (2010). Contrast gain shapes visual time. *Frontiers in Psychology*, 1, 170, doi: <https://doi.org/10.3389/fpsyg.2010.00170>.
- [151] Aaen-Stockdale, Craig, Hotchkiss, John, Heron, James, & Whitaker, D (2011). Perceived time is spatial frequency dependent. *Vision Research*, 51(11), 1232–1238, doi: <https://doi.org/>

[10.1016/j.visres.2011.03.019](https://doi.org/10.1016/j.visres.2011.03.019).

- [152] Lamme, Victor AF, & Roelfsema, Pieter R (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in neurosciences*, 23(11), 571–579, doi: [https://doi.org/10.1016/S0166-2236\(00\)01657-X](https://doi.org/10.1016/S0166-2236(00)01657-X).
- [153] Hochstein, Shaul, & Ahissar, Merav (2002). View from the top: Hierarchies and reverse hierarchies in the visual system. *Neuron*, 36(5), 791–804, doi: [https://doi.org/10.1016/S0896-6273\(02\)01091-7](https://doi.org/10.1016/S0896-6273(02)01091-7).