

**Subjective perception of ambiguous figures:
Evidence from pupillometry and
electroencephalography**

(多義図形における主観的知覚：脳波・瞳孔径計測による調査)

March 2022

Doctor of philosophy (Engineering)

Fumiaki Sato

佐藤 文昭

Toyohashi University of Technology

Date of Submission (month day, year) : March 25, 2022

Department of Computer Science and Engineering	Student ID Number D153335	Supervisors Tetsuto Minami Shigeki Nakauchi
Applicant's name Fumiaki Sato		

Abstract (Doctor)

Title of Thesis	Subjective perception of ambiguous figures: Evidence from pupillometry and electroencephalography
-----------------	---

Approx. 800 words

Our visual system receives two-dimensional information from each image on the retina. From these two-dimensional images, vision of the three-dimensional shape of the object is restored, sometimes resolving ambiguities in the visual input in an automatic and unconscious manner. In addition, human subjective visual perception is generally stable and uniquely determined. To uniquely determine perception, the brain defines and solves constraints. Since its constraints may vary from person to person, even if they see similar object, there is a possibility that different appearances occur for the individual. In the present situation, all judgments rely on subjective introspection to comprehend which appearance is seen. Today, as a global society, it is important to prevent discrepancies or misunderstandings in processing information, and seeking an index of how much can be perceived object identically is worthwhile regardless of the person seeing it. However, the technique to quantify subjective perception has not yet been established, and it is difficult to determine the index. Therefore, the quantification of subjective perception is required. In this thesis, to quantify subjective perception, I focused on the phenomenon of perceptual rivalry, primarily upon conducting three studies.

First, to clarify the relationship between attentional state and the pupil diameter during participant observed bistable figure, I performed the measurement of Steady State Visual evoked potentials (SSVEP) and the pupil diameter simultaneously. Rotating sphere stimuli composed of flickering black and white dots for tracking pupillary change, as the presentation stimulus. Resultantly, a significant difference was found in the SSVEP amplitude during left-right rotated perception. In addition, a change in pupil diameter seems to be a shift of attention target before observer response of perceptual switches. These results indicate that the shift of attention may be the trigger for the perceptual switches.

Second, I investigated perceptual bias when observing ambiguous figures using pupillometry. I hypothesized that a perceptually ambiguous or bistable object (Necker cube) can be more effectively biased, to assume a point of view-from-above (VFA) than from below the object, by cueing attention. In the results of my experiment, I found the presence of a VFA bias with forced attention, which was accompanied by reduced attentional effort, as indexed by a reduced pupil diameter, compared with the view-from-below. Conversely, participants exhibited no bias during passive viewing. Based on these pieces of evidence, I suggest that the level of intensive attention, when retrieving and maintaining a specific view from memory, is mirrored in the size of the eye pupils and may reflect ecological constraints on visual perception.

Finally, using a VR environment, I extended the second study on perceptual bias to conditions with changes in neck posture. In this study, I investigated how perceptual biases and experiential contexts of human perception affect the observer's perception when the posture is changed. I hypothesized that a change in the perceptual probability caused by perceptual bias also depends on posture. To verify this hypothesis, I focused on the Necker cube, which can be interpreted as two types of appearances from above and below despite the input remaining constant, and investigated the change of the probability of perceptual content. Specifically, I conducted the experiment by asking the observers their perception of the appearance of the Necker cube, placed at any of the five angles in VR space with pupillometry. Consequently, during the condition of looking down vertically, the probability of view-from-above perception of the Necker cube was significantly greater than during the condition of looking up. Interestingly, the pupillary results were also consistent with the probability of the perception. These results indicate that perception is modulated by the posture of the neck and suggest that neck posture is incorporated into ecological constraints.

Acknowledgements

This thesis would not have been possible without encouragement and support from many people. First of all, I sincerely would like to thank my supervisor, Prof. Tetsuto Minami, for meaningful discussions and gave me the direction of my study. I deeply appreciate Prof. Shigeki Nakauchi for giving vast ideas and precise advice. I also would like to thank Assoc. Prof. Naohiro Fukumura for evaluating this thesis with scrupulous attention to detail. I have furthermore to thank Ms. Yuki Kawai, secretary of Visual Perception and Cognition Laboratory, for supporting my students' life. I also would like to thank Prof. Bruno Laeng, University of Oslo, for always taking care of me since my bachelor's research internship. Furthermore, I sincerely appreciate him for taking meaningful discussions about my experiment, supporting my Norwegian life. Therefore, I probably wouldn't have been able to accomplish this work without his guidance. Moreover, I would like to thank my Norwegian family for giving warmest treatment and comfortable life when I was in Norway. I owe what I am today to them. I am thankful to my senior and my friends for spending a wonderful time together. In particular, Dr. Yuta Suzuki gave me many instructions for a long time since my bachelor's state. I appreciate many other seniors and friends who cannot write here. In addition, this work was supported by a Grant for Leading program: Training Brain Information Architects of Toyohashi University of Technology and JSPS KAKENHI Grant Number JP21J12947 from the Japan Society for the Promotion of Science (JSPS). Finally, I would like to express my sincere gratitude to my family and my late grandmother for their endless support, encouragement, and financial support for my students' life.

Contents

Chapter 1	Introduction	1
1.1	Background	1
1.2	What is Perceptual rivalry?	2
1.3	Brief overview of previous studies	3
1.3.1	History of binocular rivalry	3
1.3.2	History of ambiguous figure study	6
1.3.3	Recent studies of perceptual rivalry	7
1.3.4	Perceptual bias in ambiguous figures	7
1.4	Outline	8
Chapter 2	Perceptual Switches predicted by SSVEP and Pupillometry	11
2.1	Introduction	12
2.2	Method	12
2.3	Stimuli and apparatus	13
2.4	EEG recording	14
2.5	Pupil recording	14
2.6	Procedure	15
2.7	Analysis	16
2.7.1	Behavioral Analysis	16
2.7.2	EEG Analysis	16
2.7.3	Pupillary Analysis	17
2.8	Results	18
2.8.1	Behavioral Results	18
2.8.2	FFT Results	18
2.8.3	Wavelet Results	19
2.8.4	Pupillary Results	20

2.9	Discussion	22
2.9.1	Stereoscopic perception and EEG components	22
2.9.2	EEG components related perceptual switching	24
2.9.3	Interpretation of pupillary results	25
2.10	Limitation	25
2.11	Conclusion	26
Chapter 3	Pupil measurement on the cueing Necker cubes	27
3.1	Introduction	28
3.2	Experiment 1	31
3.2.1	Materials and methods	33
	Participants	33
	Stimuli and apparatus	33
	Procedure	34
3.2.2	Recording and Analysis	34
	Behavioral Analysis	34
	Pupil recording and analysis	35
3.2.3	Results	36
	Behavioral Results	36
	Pupillometry Results	37
3.2.4	Discussion	40
3.3	Experiment 2	40
3.3.1	Materials and methods	41
	Stimuli and apparatus	41
	Procedure	41
3.3.2	Recording and Analysis	42
	Behavioral Analysis	42
	Pupil analysis	42
3.3.3	Results	42
	Behavioral Results	42
	Pupillometry Results	43
3.3.4	Discussion	46

3.4	General Discussion	47
3.5	Conclusion	49
Chapter 4	The bias of ambiguous figure and posture	51
4.1	Introduction	52
4.2	Materials and Methods	54
4.2.1	Participants	54
	Stimuli and apparatus	55
	Procedure	57
4.2.2	Recording and Analysis	58
	Behavioral Analysis	58
	Pupil recording and analysis	59
4.2.3	Results	60
	Experiment 1	60
	Experiment 2	66
4.2.4	Discussion	69
	Neck posture modulates the effects of perceptual bias	69
	The size of the pupil diameter is also consistent with perception probability	70
4.2.5	Conclusion	71
Chapter 5	Conclusion	73
5.1	Summary	73
5.2	Towards the quantification of subjective perception	74
	Bibliography	77

List of Figures

1.1	An image of “#The Dress.”	2
1.2	Example of binocular rivalry stimuli.	3
1.3	Necker cube and Rubin’s vase.	4
1.4	Wheatstone’s stereoscope in 1838.	5
1.5	Patchworked rival stimuli used Kovács et al.,1996.	5
1.6	Thesis structure.	9
2.1	RDK stimuli.	14
2.2	Experimental procedure.	15
2.3	Histograms showing distributions of all participant responses.	19
2.4	Grand-average SSVEP waveforms across all participants for right/left rotation.	19
2.5	Grand-average SSVEP power across all participants for right/left rotation perception.	20
2.6	Wavelet analysis.	21
2.7	Pupil diameter in each luminance condition.	21
2.8	t test of change in pupil diameter of each condition.	22
2.9	Change in pupil diameter of the condition in which dots moved right and black dots moved to the left.	22
2.10	Change in pupil diameter of the condition in which black dots moved right and white dots moved to the left.	23
3.1	Stimuli used in Experiment 1 and 2.	30
3.2	Timeline of Experiment 1 and 2.	32
3.3	Behavioral results in Experiment 1.	37
3.4	Pupillometry results classified by perceived perspectives in Experiment 1.	38

3.5	Pupillometry results classified by perceived perspectives during nonswitch trials in Experiment 1.	39
3.6	Pupillometry results separating nonswitch trials versus switch trials in Experiment 1.	40
3.7	Behavioral results in Experiment 2.	43
3.8	Pupillometry results classified by perceived perspectives in Experiment 2.	44
3.9	Pupillometry results classified by perceived perspectives during nonswitch trials in Experiment 2.	45
3.10	Pupillometry results separating nonswitch trials versus switch trials in Experiment 2.	46
4.1	Stimuli used in Experiment 1 and 2.	56
4.2	Illustration of the timeline of the experiments.	58
4.3	Behavioral results in Experiment 1.	60
4.4	Pupillary results in Experiment 1.	62
4.5	The averaged probability of VFA perception between the cue and angle conditions across all participants in Experiment 2.	66
4.6	Pupillary results in Experiment 2.	68

Chapter 1

Introduction

1.1 Background

As we wake up in the morning, the expansive colorful world is visible in front of our eyes. The vivid view itself seems to jump into our eyes, and we do “see” the outer world casually and unintentionally, and everyone sees the colorful world upon opening their eyes. This action to process the external environment’s information as an input is driven unconsciously, and although it may sound simple, the underlying mechanism is very complicated. The retina, lining the back of the eye, captures the external information as an electric signal, and sends it to the brain for information reconstruction. Despite the fact that the image shown on the retina is two-dimensional, human beings perceive stereoscopic images restored in the brain. Additionally, human subjective visual perception is generally stable and uniquely determined. To uniquely determine perception, the brain defines and solves constraints. As its constraints vary from person to person, even upon seeing similar objects, there is a possibility that different “appearances” are perceived by the individual. For instance, the following image: “#The Dress” which became a hot topic in recent years [1], presented that we perceive the image in one of two groups, as “blue and black” or “white and gold,” even with normal color vision [2](Figure 1.1). The mechanism behind seeing different color pairs despite looking at the same image, remains unclear. Furthermore, the reason for individual differences existing is also unclear. Therefore, in the present situation, all judgements rely on subjective introspection to comprehend which “appearance” is seen.

Today, as a global society, preventing discrepancies or misunderstanding in information is critical, and it is worthy of determining an index of “how much an object can be perceived identically” regardless of the one seeing it. However, the technique to quantify “subjective perception” is not established yet, and it is difficult to identify the index. Therefore, the quantification of “subjective perception” is required.

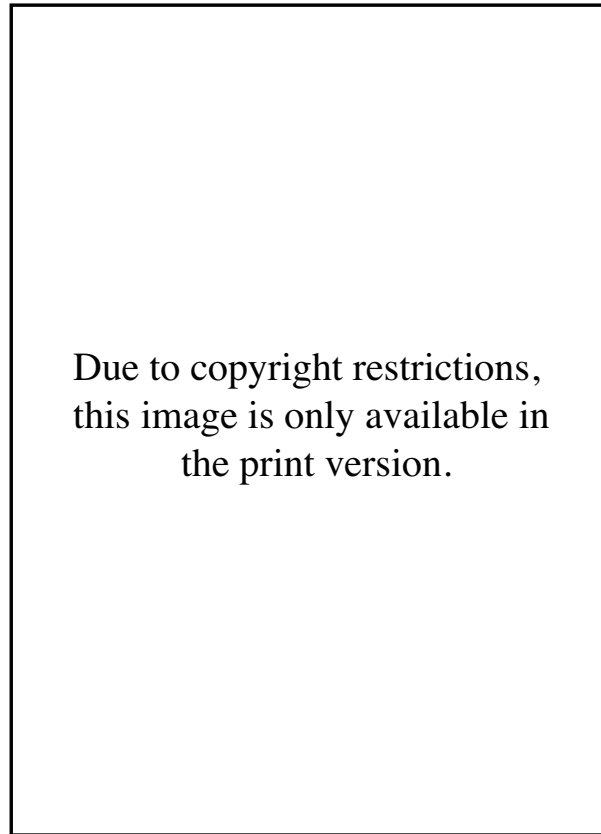


Fig. 1.1: An image of “#The Dress” [1].

In this study, to quantify “subjective perception,” I focused on the phenomenon of perceptual rivalry. This phenomenon will be explained in the following section.

1.2 What is Perceptual rivalry?

Human subjective visual perception is generally stable and uniquely determined. However, there are exceptions, one of which is known as the phenomenon of perceptual rivalry, where multiple perceptual appearances occur even though the visual input to the eyes remain constant. There are roughly two types of phenomena that cause perceptual rivalry. One is called binocular rivalry, which is when both monocular eyes are given separate inputs, which are not perceived simultaneously, but alternately. Figure 1.2 shows an example of the stimuli used in previous studies. The other is a perceptual rivalry triggered by ambiguous figures like a Necker cube or Rubin’s vase (Figure 1.3). These two phenomena have many common characteristics, along

with differences, and they have contributed to the advancement of the mechanism of perceptual switches.



Fig. 1.2: Example of binocular rivalry stimuli cited from [3].

If the image on the left side is the input to the left eye, and the image on the right is for the right eye, it can be perceived alternately.

A characteristic of perceptual rivalry is that the input information does not change, but the perceptual change that occurs may be able to account for the problem of how perception is processed in the brain; research in this phenomenon has been conducted for the past 30 years. The next section provides a brief overview of previous studies on perceptual rivalry.

1.3 Brief overview of previous studies

1.3.1 History of binocular rivalry

Historically, binocular rivalry was reported in the 16th century by Giambattista della Porta, a renowned Italian polymath [6, 7]. The English translation of the Italian book by Wade in 1998

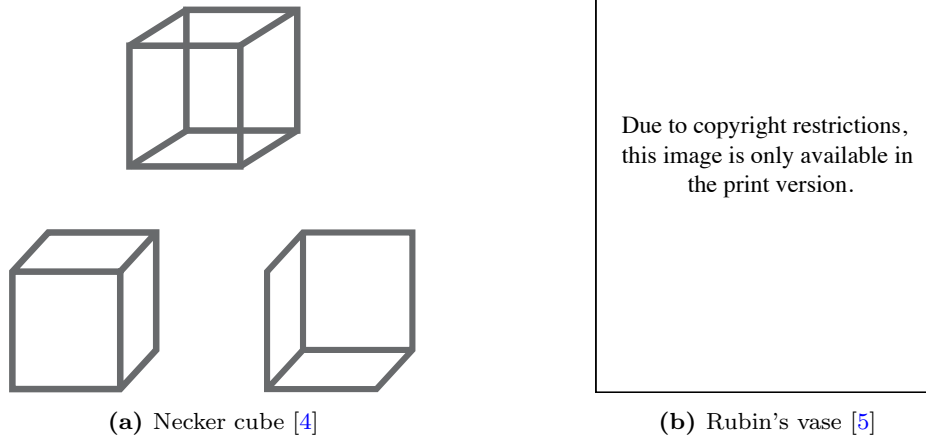


Fig. 1.3: Necker cube and Rubin's vase

(a) The cube in this figure can be interpreted as two types, upward and downward, but not both simultaneously. (b) Rubin's vase induces the appearance of either a face or a vase. These figures are called "ambiguous figures" or "bistable figures."

specified the following: "..., we always see with one eye, even if we think both are open and that we see with both. We may prove it by these arguments: To separate the two eyes, let us place a book before the right eye and read it; then if someone shows another book to the left eye, it is impossible to read it or even see the pages, unless for a short moment of time the power of seeing is taken from the right eye and borrowed by the left." quoted from Wade, 1998 [7]. Similar to this example, it has long been known that it is impossible to see separate information with both eyes simultaneously. Still, it was not until much later, that this phenomenon was studied more systematically.

The study of the binocular rivalry was systematically initiated by Wheatstone in 1838, when a paper on stereoscopes for viewing a stereoscopic pair of images was published in the process of studying stereoscopic vision [8, 9] (Figure 1.4). Since then, many psychologists such as Helmholtz [10, 11] and William James [12] have been fascinated by this phenomenon, and have studied, considered, and explained it. As for modern experiments on the binocular rivalry paradigm, it was in Breese's study [9, 13, 14] that a red square was presented to the right eye and a green square in the left eye. Subjects responded to their perception using the corresponding key to the stimulus. This paradigm made it possible to quantify the dwell time of the rivalry per 100 seconds.

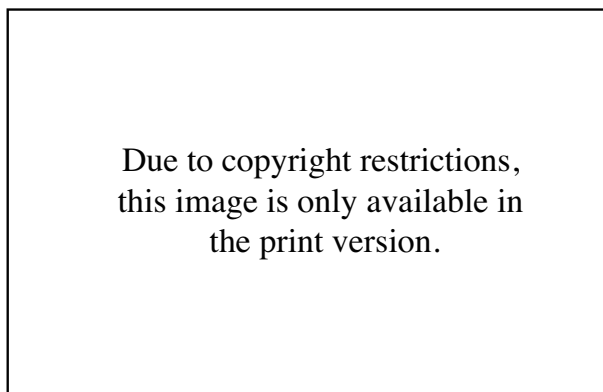


Fig. 1.4: Wheatstone's stereoscope in 1838 (cited from [8]).

From various subsequent studies until the 1980s, the view of this mechanism was called “eye-based rivalry,” which held the view that monocular neurons suppressed another neuron in one of the places where pathways from the retina led to the early visual cortex [9, 15]. However, in the late 1990s, the emergence of two landmark paradigms and improvements in brain activity measurement technology suggested the involvement of other mechanisms in binocular rivalry. In a landmark study, Kovács et al. devised patchworked rival stimuli consisting of two complex image fragments. An example is a pair below, as shown in the Figure 1.5. The participants could experience reassembled stimuli into coherent forms. This demonstration suggested interocular grouping, which is more than mere eye competition [15, 16]. In another study, the effect of rapidly switching rivalry stimuli between the two eyes was tested. Under this condition, the rate of perceptual switch showed similar dynamics as static stimuli, despite the rapid switching of stimuli [17]. The results of this study also cannot be explained merely by eye-based rivalry.

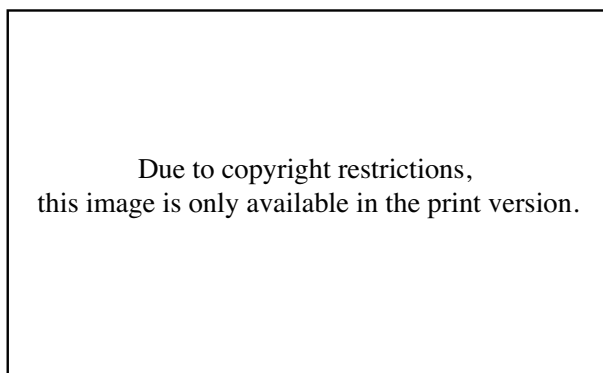


Fig. 1.5: Patchworked rival stimuli used Kovács et al., 1996 (cited from [16]).

The recent generic view is that eye-based rivalry and stimulus rivalry are distinct phenomena;

however, closely related processes arise from neural events spread over multiple stages of the visual hierarchy [3, 15, 18–20].

From the 1990s, brain activity measurement during binocular rivalry was actively conducted based on the possibility of discovering neural correlates of consciousness by studying brain activity that correlates with subjective perception [21, 22]. Improvements in brain measurement techniques such as functional magnetic resonance imaging (fMRI) and electroencephalography (EEG) also help increase these studies on brain activity measurement.

1.3.2 History of ambiguous figure study

Typical discoveries of ambiguous figures were further after finding binocular rivalry, mainly in the 19-20th century. The Necker cube was first published in 1832 [4], and the Rubin vase, in 1915 [5]. In the field of psychology, this mechanism of ambiguity was attempted to be interpreted by the framework of “Gestalt psychology,” whose core idea is perceptual grouping that is essential for recognizing objects(see also review [23]). In particular, the perception of an ambiguous figure such as Rubin’s vase is called “figure-ground perception,” and when focusing on the white part, the black part is recognized as the background and vice versa. In addition, only one object is recognized [24–26]. Moreover, in the early 1900s, experiments using ambiguous figures such as Necker Cube had already been conducted to discuss perceptual instability [27–29]. Importantly, the top-down [30] and bottom-up [27]) processes had already been discussed based on the results of the reversal rate of Necker cube from an early stage. The top-down process refers to that which is hypothesized to be obtained from assumptions of past experience and prior knowledge, and the bottom-up process refers to that which is caused by sensory input. (See also reviews [29, 31], and the introduction of [32] for multiple other early studies.) Since the 1990s, brain activity measurements during ambiguous figure observation were actively performed, as in the study of binocular rivalry.

1.3.3 Recent studies of perceptual rivalry

An early study of binocular rivalry using fMRI revealed differences in the prefrontal cortex activity due to differences in subjective perception, despite a constant stimulus [33]. Subsequent studies of perceptual rivalry have also suggested that the prefrontal cortices, such as dorsolateral prefrontal cortex, medial prefrontal cortex, and superior precentral sulcus (or the frontal eye field) are associated with brain activity that correlates with subjective perception (fMRI study: [34–38], EEG or MEG studies: [37, 39, 40], Review: [41–46]). Conversely, recent studies have argued that the prefrontal cortex is more closely related to introspection, such as the behavioral report by subjects, rather than perceptual switches [47–49] (Review: [50, 51]). This issue, which has not attained consensus for many years, suggests the difficulty of separating subjective perception from other brain activities.

The debate on whether the requirement of attention for perceptual switches is another important issue on which there is no consensus. Some studies have suggested that attention is required for perceptual switches [52], while others have suggested that attention is not required [53]. It is also an important viewpoint that attention is not always required for the process of consciousness or V1 activities in the human brain [54–56].

Other than brain activity, eye movements and pupillary responses are also important for the estimation of subjective visual perception, as physiological indicators. In recent years, studies have reported using optokinetic nystagmus (OKN), which is an eye movement, as a surrogate index for reporting [48], and studies in which perceptual switches are estimated from the pupillary response by using luminance difference [57, 58]. A finding also suggests that the pupil diameter dilates when perceptual switches occur [59].

1.3.4 Perceptual bias in ambiguous figures

Ambiguous figures with multiple appearances that cause perceptual rivalry are known to cause biases in the preferences of these appearances. As a way of resolving perceptual ambiguity, Nakayama and Shimojo (1992) proposed a theoretical framework in which the visual system

tends to interpret images and surfaces as seen from a generic point, instead of an accidental vantage point [60]. In other words, the object properties of ambiguous images are estimated based on constraints derived from past visual experiences.

Several visual generic principles have been proposed for disambiguating the perception of objects (e.g., the light-from-above constraint; [61]). The view-from-above (VFA) constraint or heuristic is a bias in vision that results when the input information is ambiguous and consistent with different viewpoints on a single object [62], the VFA is preferred in perception over the alternative view-from-below.

Kornmeier and colleagues suggested that observers prefer the VFA due to an asymmetry of perceptual experiences or statistical learning, according to which we more often look down on objects (e.g., artifacts) than we look up at them [63]. Remarkably, Sundareswara and Schrater (2008) showed that the VFA preference for Necker cubes is close to 100% for very short presentations and declines for prolonged exposures, but it remains the most likely interpretation. As these authors have indicated, in Bayesian models of perception, the visual system tends to choose the optimal interpretation among the available alternatives, typically the viewpoint with maximal posterior probability [64]. Hence, a Bayesian account suggests that VFA may be the most frequent experience with many types of common objects, which are usually manipulated at the hand level, and therefore examined from a top view. Supposedly, the Necker cube may be spontaneously interpreted as a representation of some kind of smaller-than-the-body box that could be “afforded” by the hands.

1.4 Outline

In this thesis, I discuss the phenomena of perceptual rivalry from experiments measuring electroencephalogram (EEG) and eye movements with their respective analysis. The first chapter (this chapter) gives an overview of this thesis and introduces related research on perceptual rivalry. In Chapter 2, I describe an experiment in which EEG and eye movements are measured during the presentation of a stimulus consisting of Random Dot Kinematogram (RDK), which induces perceptual switches. In Chapter 3, I present the relationship between pupillary response and the perceptual bias of perceptual switch. Finally, in Chapter 4, I comprehensively discuss

and summarize my study. Figure 1.6 shows an outline of this thesis, composed of five chapters.

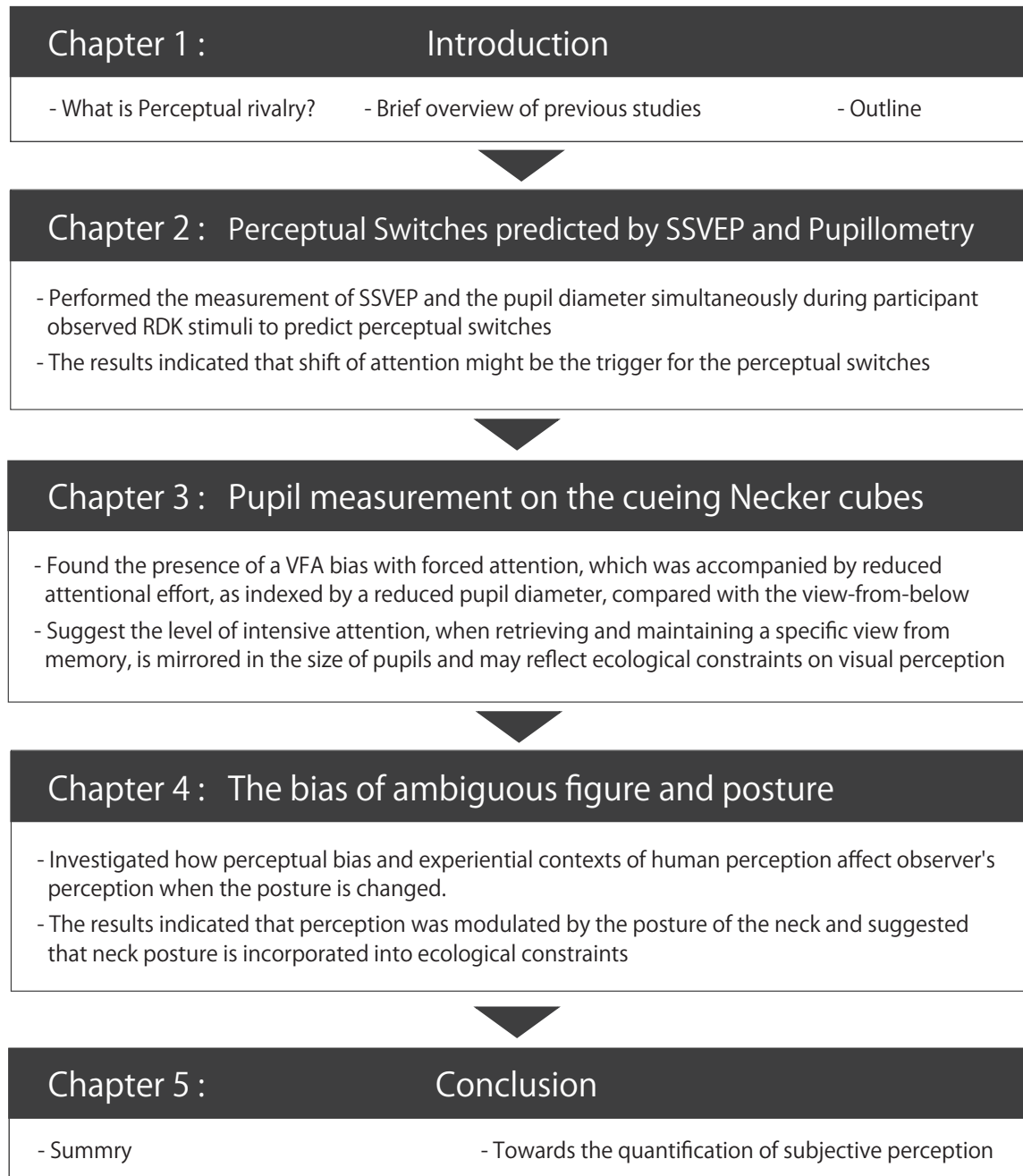


Fig. 1.6: Thesis structure.

Chapter 2

Perceptual Switches predicted by SSVEP and Pupillometry

A similar Japanese version of this chapter has been published as:

佐藤文昭, 鈴木雄太, 中内茂樹, & 南哲人. (2018). 定常状態視覚誘発電位と瞳孔計測を用いた知覚交替情報の抽出に関する研究. 電子情報通信学会論文誌 D, 101(3), 607-614.

(English title: Fumiaki Sato, Yuta Suzuki, Shigeki Nakauchi, and Tetsuto Minami (2018), Predicting Perceptual Switches Using SSVEP and Pupillometry. The transactions of the Institute of Electronics, Information and Communication Engineers. D,101(3),607-614)

2.1 Introduction

As shown in Chapter 1, recent studies have revealed changes in brain activity and pupillary response before and after perceptual switches. Parkkonen and colleagues estimated attentional shift as perceptual switches using the steady-state visual evoked potential (SSVEP), which is an EEG component induced by flickering stimuli, and showed that the SSVEP power changed before and after the perceptual switches [65]. Einhäuser and colleagues showed that the pupil diameter dilated during the perceptual switches [59]. The relationship between changes in attentional targets observed via the SSVEP and pupil dilation when perceptual switches, is still unclear. Binda and colleagues have shown that it is possible to estimate attentional targets by pupillometry with different luminance values [66].

From these pieces of evidence, if the change in the target of attention is related to perceptual switches, it may be possible to extract the change in pupil diameter by pupillometry using the luminance difference. If the change of the attention target can be extracted in the pupil diameter, it may be possible to obtain new knowledge about the temporal dynamics of the attentional state and the perceptual switch by comparing these dilations' latency.

Therefore, the purpose of this study was to investigate the factors that cause the perceptual switches by focusing on the changes in the attention target of the early visual cortex and the pupil dilation at the timing of the perceptual switches. Specifically, the attention target was estimated using stimuli with different luminance and flickering frequencies. I used the SSVEP to confirm that the attention state changes in the rotating sphere stimulus as in the previous findings, and to confirm that whether the attention state of the early visual cortex and the pupil are consistent.

2.2 Method

Ten subjects participated in Experiment 1. All participants self-reported that they had a normal or corrected-to-normal visual acuity. The experimental procedures received approval from the Committee for Human Research at the Toyohashi University of Technology. Participants provided written informed consent, and the experiment was conducted in accordance with the guidelines of the committee.

2.3 Stimuli and apparatus

Stimuli were based on the random dot kinematogram (RDK) stimuli used in previous studies [67, 68], which are called ambiguous figures and are known to perceive the dots as spheres that are physically moving in a horizontal plane, but rotating in either a clockwise or counter-clockwise manner. To simulate a rotating sphere by all dots, the velocity of one of the dots was set to $1/2\pi$ [deg/sec] (moving to the left), and the velocity of the other group of dots was $-1/2\pi$ [deg/sec] (moving to the right).

To induce a change in pupil diameter as the target of attention shifted, the two groups of dots were given different luminance values (dark: 0.28 [cd/m²], bright: 80.06 [cd/m²]). The background luminance was set to 40.38 [cd/m²], which was the average luminance of the two types of dots. Depending on which dot group was rendered first, the physical properties of the stimuli were slightly different. Therefore, two stimuli in a different drawing order were used (Figure 2.1).

The total conditions of this experiment consisted of four sub-conditions: two conditions in the direction of movement of the dots, and two in the order in which the dots were drawn, in each luminance. To induce SSVEP, the leftward-moving dots flickered at 7.5 Hz while the rightward-moving dots flickered at 6 Hz. A fixation cross ($0.4\text{deg} \times 0.4\text{deg}$) was presented at the center of the stimulus.

The experiment was conducted in a darkroom, and the stimuli were presented to the participants on an LCD monitor (ViewPixxEEG, VPixx Technologies, Resolution: 1920×1080 pixels, FrameRate: 120 Hz). Participants were seated with their heads held in place by a chin rest and their viewing distance was 60 cm. The task was executed in MATLAB 2015b (The MathWorks, Natick, MA) using Psychtoolbox3 [69].

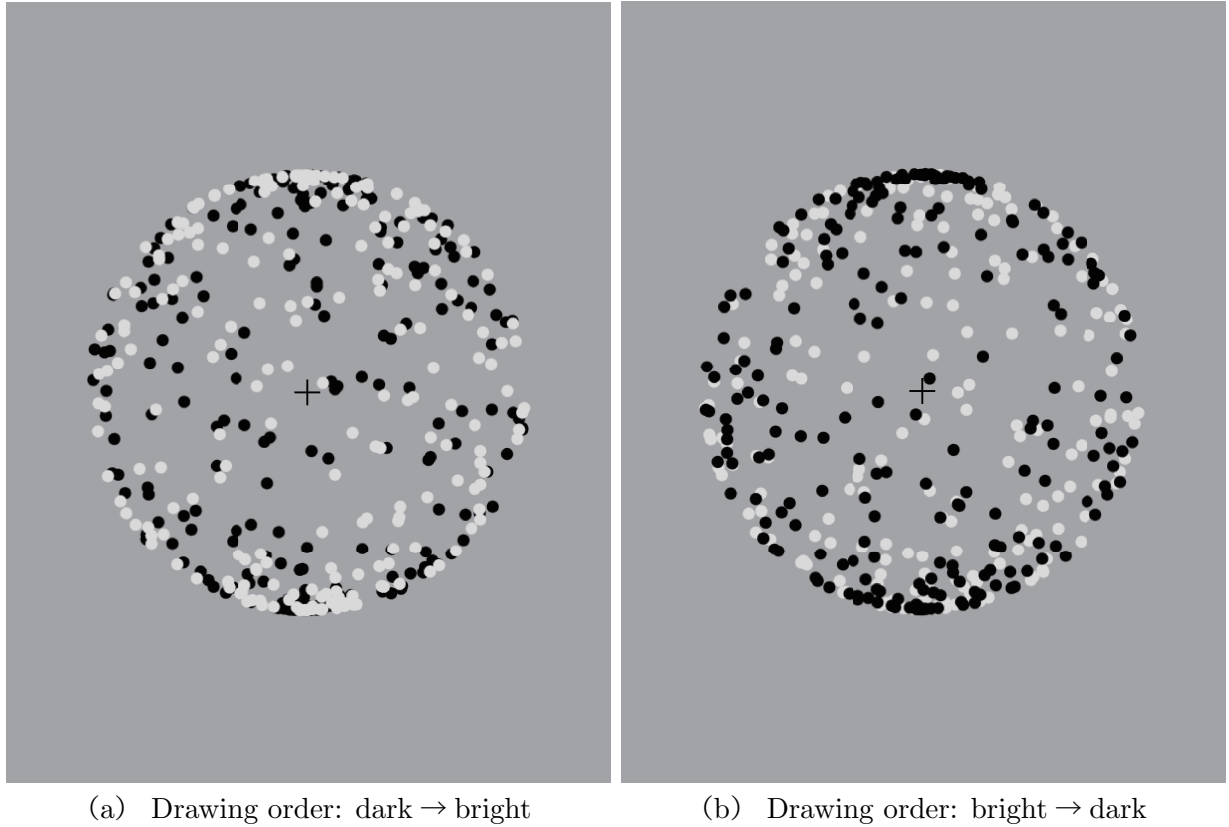


Fig. 2.1: RDK stimuli. ©2018 IEICE

2.4 EEG recording

EEG activity was measured using the Biosemi Active two 64 electrode (BioSemi Inc., Amsterdam, The Netherlands) referenced online to the vertex (Cz) and six extra channels. The data were measured at a sampling frequency of 512 Hz. The measuring electrodes were arranged in accordance with the International 10-20 system. Extra electrodes were applied horizontally and vertically to the eye, for bipolar monitoring of blinks. All electrode impedances were reduced to less than 20 k Ω .

2.5 Pupil recording

The pupil size and eye movements were measured during the task using an eye-tracking system (EyeLink 1000, SR Research, Oakland, Canada) at a sampling rate of 500 Hz. Eye movement was observed in the participants' left eye with an infrared light video camera at a resolution of no more than 0.1.

2.6 Procedure

The fixation cross was presented for 5 seconds, and then the RDK stimulus was presented for 10 minutes. Participants gazed at the fixation point with both eyes and respond to the direction of rotation that they perceived immediately after the stimulus was presented. Thereafter, whenever the perceived direction of the rotation switched, participants were instructed to respond with a button corresponding to the perceived direction. When the direction of rotation was perceived to be clockwise, the '4' key was pressed, and when it was counterclockwise, the '6' key was pressed.

The experiment was conducted after a training session for the perceptual switching for 10-minutes. Four sessions were conducted in the whole experiment, with one session per condition. The flow of one trial is shown in Figure 2.2.

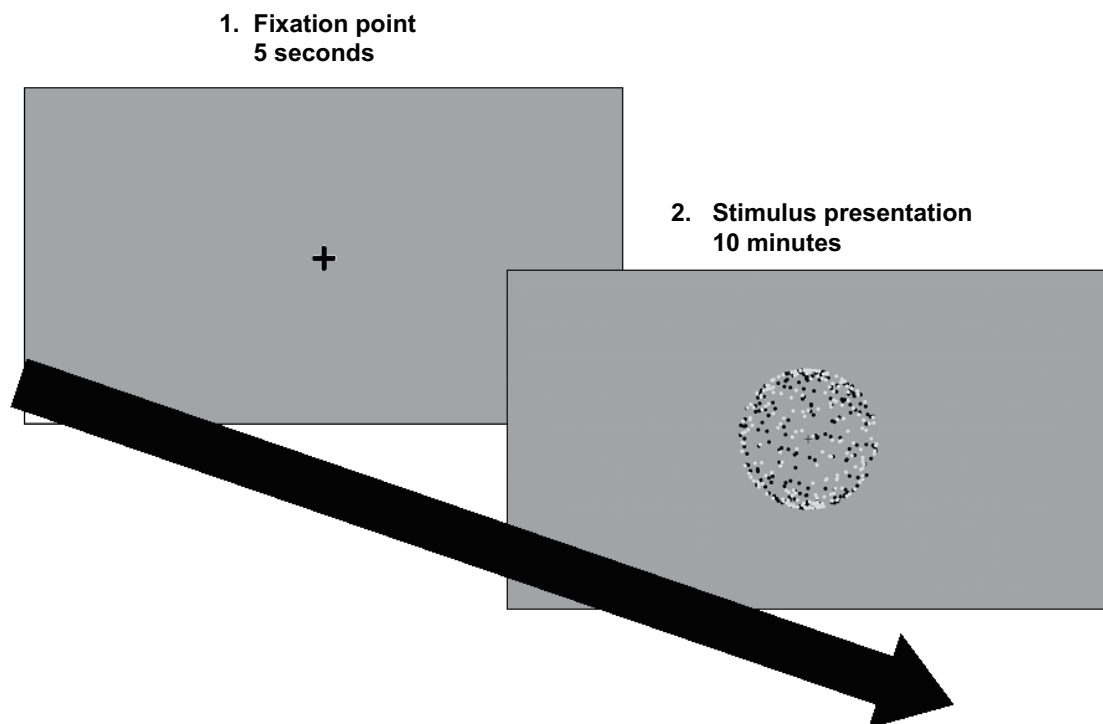


Fig. 2.2: Experimental procedure. ©2018 IEICE

2.7 Analysis

The analysis software used was Matlab 2015b (MathWorks) and EEGLAB 13.6.5b [70] were used. The analysis is divided into three sections: behavioral analysis, EEG analysis, and eye movement analysis, as described below.

2.7.1 Behavioral Analysis

The sum of the number of the participants' responses is shown in a histogram and was fitted with a gamma function. Response intervals of 100 seconds or more were considered outliers, and excluded.

2.7.2 EEG Analysis

The continuous EEG data were band-pass filtered from 1–30 Hz after being re-referenced to an average using the EEGLAB toolbox (Delorme and Makeig, 2004). To remove artifacts in the EEG signal, independent component analysis of Faster's method [71] was implemented to correlate the blink signal with the EEG.

FFT Analysis

After the pre-processing, the EEG data epoched for each experimental condition (four conditions) separately for each perception (clockwise or counterclockwise) of the participants. As the way which the participants perceived just before pressing the button is unclear, the data of 500 ms before pressing the button was removed. Subsequently, the epoched data was transformed to the frequency domain by fast Fourier transform. A certain level of frequency resolution is required to confirm the power of the stimulus flickering frequencies of 6 Hz and 7.5 Hz; therefore, the epoched data that were less than 6 seconds in length, excluding the 500 ms before the button press, were excluded from the analysis. For data longer than 6.5 seconds, the 500 ms immediately before the pressing the button was excluded, and the data for 6 seconds after the button

was pressed was set as the analysis window. The obtained SSVEP power was normalized by the maximum SSVEP power in the frequency band of 4 Hz or more, excluding the background EEG. The topographical map of the grand-averaged SSVEP amplitudes at each electrode location showed peak activity in the occipital area. Therefore, five occipital electrodes (O1, Iz, Oz, POz, and O2) were selected and averaged as the amplitudes of the channels. Subsequently, the data were averaged across conditions and then grand-averaged across participants. Thereon, the t-test was conducted to confirm for statistically significant differences between the SSVEP power in the 6 Hz and 7.5 Hz bands during clockwise and counterclockwise perception.

Wavelet Analysis

The data for 3 seconds before and after the participant's response (displayed for 2 seconds before and after) fitted to the phase of 7.5 Hz and 6 Hz, respectively, and was analyzed using the Morlet wavelet method (12 cycles). The analysis was performed using five occipital electrodes as similar to the FFT analysis. The time width was in 10 ms increments. The time to frequency transformations were performed after the trials were averaged. The fieldtrip toolbox [72] was used for the analysis. In this experiment, the response time was not determined, so the SSVEP phase at the timing of response varied from trial to trial. Therefore, additive averaging offsets the important EEG components. To address this problem, the phase-matching method was adopted in this analysis. In case the trial was adjusted to 7.5 Hz, the phase was adjusted by changing the trigger signal at the timing of the response to the nearest value at which the phase at 7.5 Hz became zero. The same process was performed at 6 Hz. From the powers obtained wavelet analysis in the 7.5 Hz and 6 Hz bands with the phases, adjusted for each condition, as they were segmented out, normalized by the maximum value in each frequency band, averaged between conditions, and showed the values for each response direction.

2.7.3 Pupillary Analysis

In the pupillary analysis, the rate of change in pupil diameter before and after the perceptual switching was calculated. The data was complemented using linear interpolation for the blinking region of the measured pupil diameter data. Next, the value of 100 milliseconds from 3.1 seconds

to 3.0 seconds before the participant response was used as the baseline, and the pupil diameter data of each participant was divided by the average of the baseline. Subsequently, thresholding was used to exclude trials that included values with a pupil diameter change rate of 0.7 or less, and 1.5 or more. By this threshold processing, it was judged that the data of the pupil diameters of the two subjects whose trials were excluded by 50% or more were not properly obtained, and they were rejected from the analysis. The rate of change in pupil diameter 3 seconds before and after the participant response was averaged between trials for each brightness condition, and grand-averaged across the participants. To confirm a statistically significant difference between the pupil diameter when perceiving clockwise and counterclockwise before perceptual switching, we calculated the average of the pupil diameter change rate from 1 second to 2 seconds before each response, and performed a t-test. Additionally, to confirm whether pupil dilation occurs during perceptual switching, we calculated the average of the pupil diameter change rate from 3 seconds to 2 seconds before, and the average value of the pupil diameter change rate from 0 seconds to 1 second. A t-test was performed for each brightness condition and each response.

2.8 Results

2.8.1 Behavioral Results

Figure 2.3 shows the results of the gamma distribution that approximated the probability distribution of all experimental participant responses. As shown in Figure 2.3, it was confirmed that the gamma distribution can be approximated.

2.8.2 FFT Results

Frequency analysis was performed on the EEG during clockwise and counterclockwise perception in all conditions. Figure 2.4 shows the averaged SSVEP power in the frequency band across participants. The colored shade represents the standard error. Figure 2.5 shows the t-test results of the SSVEP power in the 6 Hz and 7.5 Hz bands when perceiving each rotation. In the result of the 6 Hz band, there was a significant difference between clockwise and counterclockwise perception $t(9) = -2.948$, $p = 0.0163$, $r = 0.70$, $d = 0.39(p < 0.05)$. Similarly, there was a significant difference between the rotation perceptions in the 7.5 Hz band $t(9) = 2.946$, $p = 0.0163$, $r = 0.70$, $d = 0.35(p < 0.05)$.

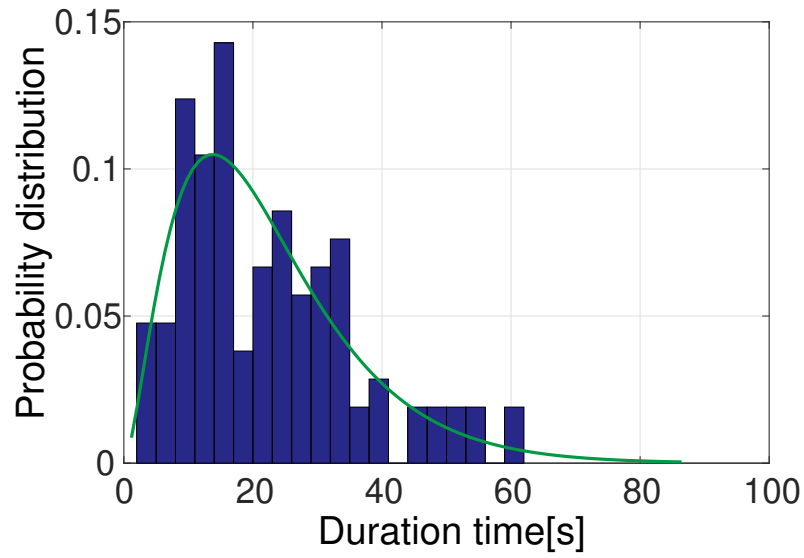


Fig. 2.3: Histograms showing distributions of all participant responses. ©2018 IEICE

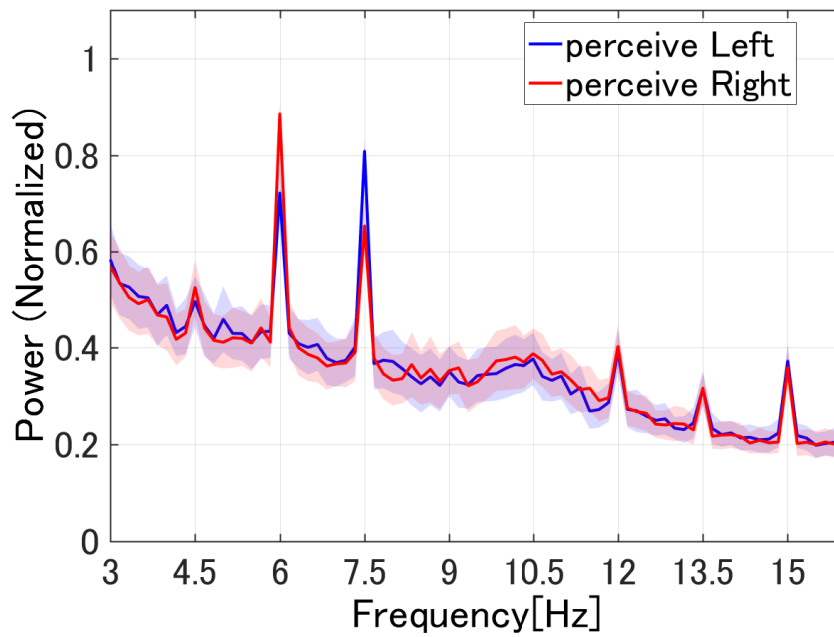


Fig. 2.4: Grand-average SSVEP waveforms across all participants for right/left rotation. ©2018 IEICE

2.8.3 Wavelet Results

Figure 2.6 shows the results of the wavelet analysis averaged across the participants 2 seconds before and after each response. The colored shade represents the standard error. In Figure 2.6,

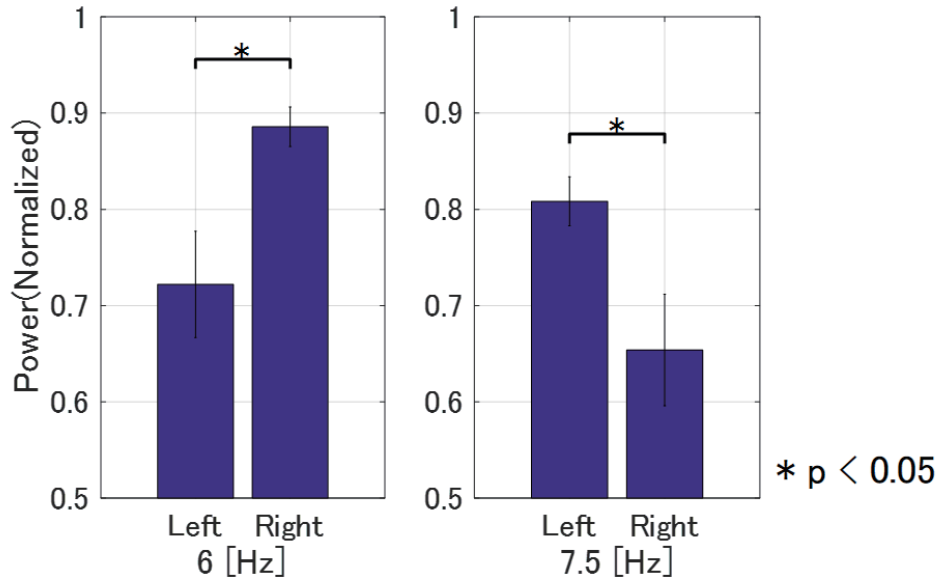


Fig. 2.5: Grand-average SSVEP power across all participants for right/left rotation perception. ©2018 IEICE

it was confirmed that the SSVEP power at 7.5 Hz was higher than that at 6 Hz after 0 seconds in the response of left(perceived clockwise). It was also confirmed that the SSVEP power at 6 Hz was higher than the SSVEP power at 7.5 Hz during the right response before around 1 second.

2.8.4 Pupillary Results

Figure 2.7 shows the grand grand-average of the change rate in pupil diameter in 3 seconds before and after the response across participants. The colored shade represents the standard error.

Figure 2.8 shows the result of t-test for each brightness condition for the change rate in pupil diameter between each response from -2 seconds to -1 second. Although neither significant difference was obtained, it was confirmed that when the brightness condition was reversed; the magnitude of the change rate in pupil diameter between each response was also reversed. The average of change rate in pupil diameter from -3 seconds to -2 seconds (hereinafter, a) and the average of change rate from 0 seconds to 1 second (hereinafter, b) were compared with a t-test. The results are shown in Figure 2.9, Figure 2.10. As shown in Figure 2.8, there was a significant

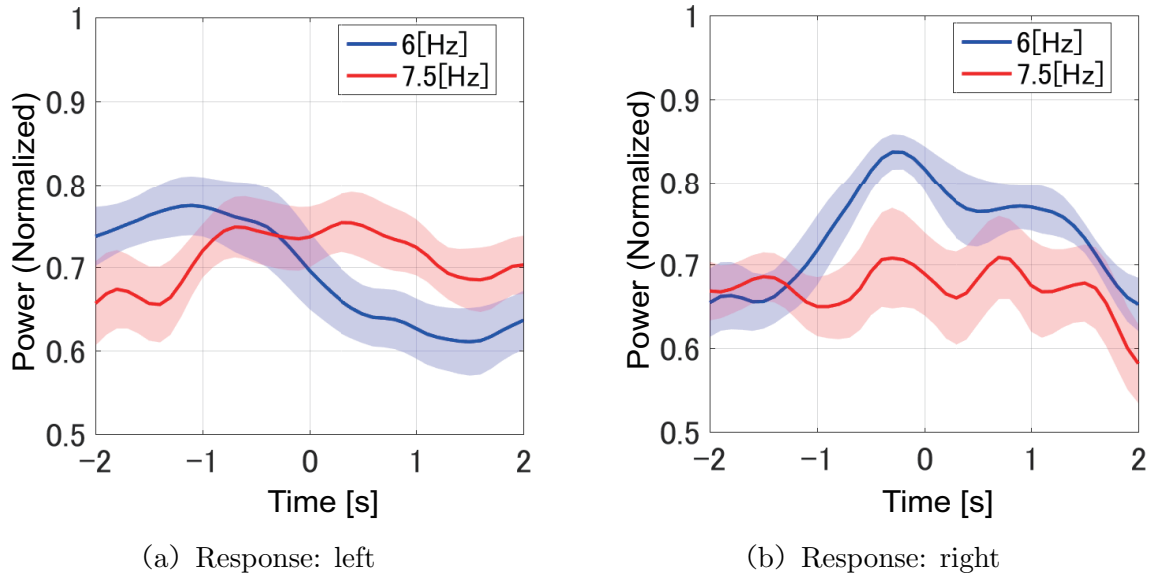


Fig. 2.6: Wavelet analysis. ©2018 IEICE

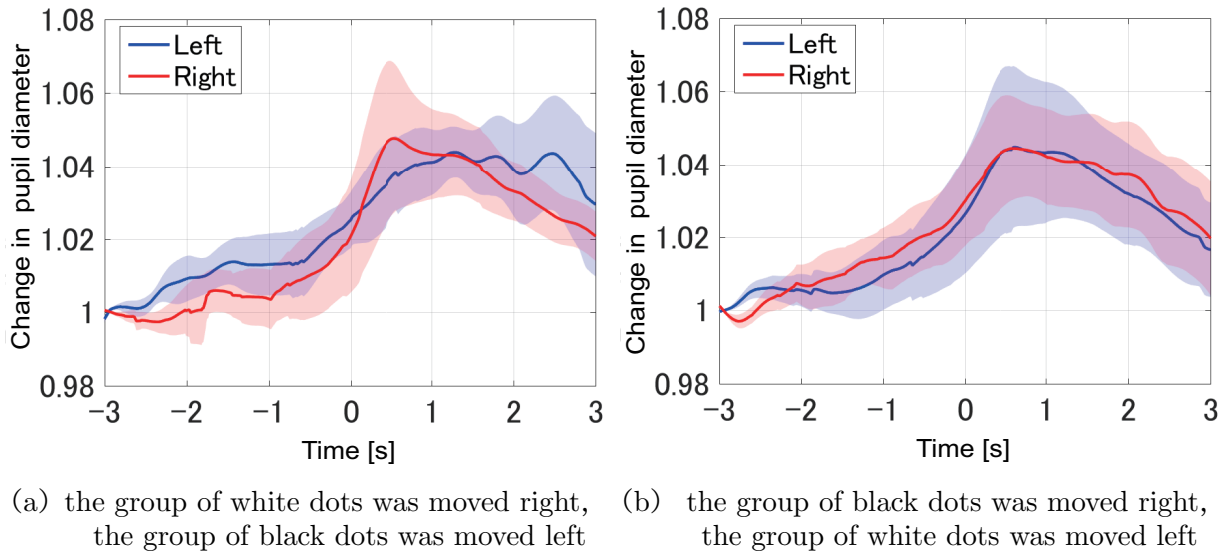


Fig. 2.7: Pupil diameter in each luminance condition. ©2018 IEICE

tendency in both the left and right response. (left response: $t(7) = -2.3662$, $p = 0.0502$, $r = 0.67$, $d = 1.01$, right response: $t(7) = -2.1166$, $p = 0.0721$, $r = 0.63$, $d = 0.97$). As shown in Figure 2.10, there was a significant tendency in the left response and a significant difference in the right response before and after perceptual switching (left response: $t(7) = -2.0481$, $p = 0.0798$, $r = 0.61$, $d = 0.80$, right response: $t(7) = -3.0644$, $p = 0.0182$, $r = 0.76$, $d = 1.19$).

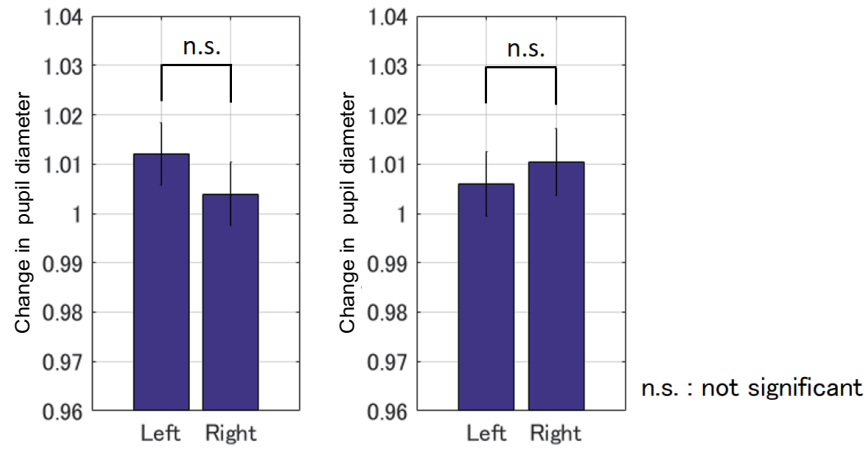


Fig. 2.8: t test of change in pupil diameter of each condition. (a) the group of white dots was moved right, the group of black dots was moved left. (b) the group of black dots was moved right, and the group of white dots was moved left. ©2018 IEICE

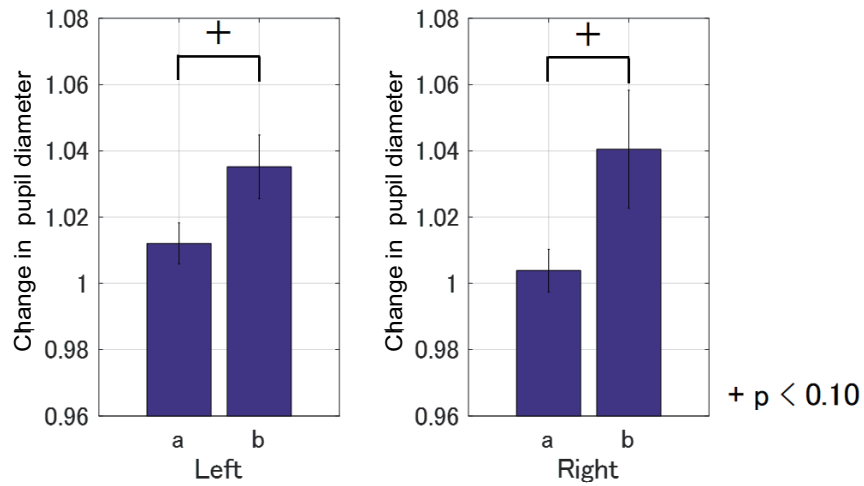


Fig. 2.9: Change in pupil diameter of the condition in which dots moved right and black dots moved to the left. ©2018 IEICE

2.9 Discussion

2.9.1 Stereoscopic perception and EEG components

As depicted in Figure 2.3, it was confirmed that the gamma distribution was approximated. This is consistent with the report by Krug et al. [73] that the interval of perceptual switching is approximated to the gamma distribution in a long-term task.

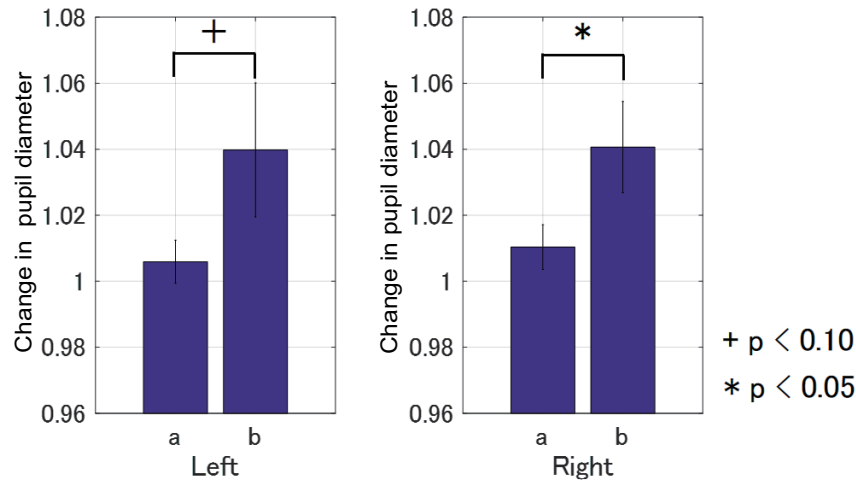


Fig. 2.10: Change in pupil diameter of the condition in which black dots moved right and white dots moved to the left. ©2018 IEICE

The SSVEP is known to be evoked at a flickering frequency of the stimulus and an integer multiple of that frequency. Therefore, in Figure 2.4, a method of analyzing the 12 Hz and 15 Hz which is harmonics of 6 Hz and 7.5 Hz is also conceivable. In fact, peaks were seen at 12 Hz and 15 Hz in Figure 2.4. However, robust power was obtained at the flicker frequency of the stimulus than at harmonics compared to the adjacent frequency band, and it is considered sufficient to analyze only the flicker frequency of the stimulus.

Furthermore, in Figure 2.4, a peak was seen in the SSVEP power at 13.5 Hz for both perceptions of clockwise and counterclockwise rotation. According to the report by Gundlach et al., when there are two figures with different blinking frequencies and the subjective contour is recognized by combining the two figures, the SSVEP power of the frequency which is added two flickering frequency corresponding two figures had a peak [74]. As a peak was found at 13.5 Hz, which is the sum of the two frequencies of 6 Hz and 7.5 Hz presented in this experiment, similar results were obtained by Gundlach et al. for stereoscopic perception, and the two types of dots were recognized as a single sphere.

2.9.2 EEG components related perceptual switching

In Figure 2.4, there was a significant difference in the SSVEP power in the 6 Hz and 7.5 Hz bands between participant's perception of the clockwise and counterclockwise rotations. In this study, to exclude the effect of the button press, we excluded the 500 ms immediately preceding the button press. The reason for excluding these 500 ms is that the simple reaction time for button pressing in cognitive experiments generally takes 150 to 300 ms [75]. In some previous studies, the simple reaction time exceeded 300 ms, depending on the task and experiment participants [76]. However, unless the participants were elderly, studies exceeding 500 ms had not been reported.

In addition, from Figure 2.6(a), the magnitude of the SSVEP amplitude in the 6 Hz band and the 7.5 Hz band were reversed from about 1 second before the button response. It was implied that when participants perceived the direction of rotation of the stimulus change from counterclockwise to clockwise, their attention were shifted from the 6 Hz dots to the right, to 7.5 Hz dots which were moved to the left. In Figure 2.6(b), there is no reversal as shown in Figure 2.6(a), but the power amplitude in the 6-Hz band increases by approximately 1 second before the button response. It is implied that when participants perceive counterclockwise rotation, they pay attention to the 6 Hz dots which move to the right. These results may be reasonable given that the subject is paying attention to the dot in front. In addition, although the presented stimulus is constant, the SSVEP amplitude changes with perceptual switching. The fMRI study by Freeman et al., suggested the possibility of feedback of higher-order information to the early visual cortex [77]. Therefore, changes in the SSVEP amplitude, as shown in Figure 2.4, can have changes from Lateral Occipital Complex (LOC) and other higher-order visual areas to early visual area.

Watanabe et al. reported that activity in the early visual cortex reflects attention, but not consciousness [54]. Therefore, it is suggested that no perceptual switching has yet occurred at the time of the change in the attentional target, and it is possible that a change in the attentional state may trigger perceptual switching.

2.9.3 Interpretation of pupillary results

In Figure 2.7(a) and (b), approximately 2 seconds before the response, the pupil diameter between perception of rotation was reversed by difference of luminance in stimulus. It is implied that the participants pay attention to the dots which is moved in the same direction as the front of rotation. However, no significant difference in the rate of pupil diameter change prior to perceptual switching was observed. This may be because the onset of the perceptual alternation differed from trial to trial, and the change in pupil diameter was not successfully observed in the additive mean. It may also reflect the effect of button presses [59].

The rates of pupil change from -3 seconds to -2 seconds and from 0 to 1 second from button press in Figure 2.9 and 2.10, was a significant difference, indicating pupil dilate in the vicinity of 0 seconds. This is consistent with Einhauser et al.'s previous finding that the pupil diameter dilates by perceptual switching. Since the dilation of perceptual switching occurs after the attention shifted to the dots that move in the front as the rotation direction perception, it is suggested that perceptual switching is triggered by the change of attention by the unconscious.

2.10 Limitation

In this study, the change in pupil diameter seemingly reflected attentional switching, but there was no significant difference. Therefore, a future consideration is to improve the experimental design and perform pupil measurement in the condition when disturbance is absent. Specifically, since the SSVEP has been shown to accurately estimate the rotation perception in this study, it is considered a key method for identifying the perception of rotation direction, instead of relying on a behavioral report by button press. In such an experimental design, more accurate extraction of perceptual switching information must be conducted without including the influence of button-pressing.

2.11 Conclusion

The aim of this study was to extract the information that causes perceptual switching by using RDK stimuli measuring EEG and pupil diameter. I investigated the relationship between attention and perceptual switching. In our experiments, I attempted to estimate the attentional state using a group of dots with different frequency and luminance. Resultantly, there was a significant difference in the SSVEP amplitude during the perception of each rotation. From this evidence, it is suggested that the attention target shifted during the perceptual switching in RDK stimulus. There was a change in the pupil diameter upon change of target of attention, and this change was observed from an early stage of perceptual switching. After that, the pupil dilation occurred due to perceptual switching. From these results, it was suggested that perceptual switching may be triggered by the shift of attention under unconsciousness.

Chapter 3

Pupil measurement on the cueing Necker cubes

A similar version of this chapter has been published as:

Fumiaki Sato, Bruno Laeng, Shigeki Nakauchi and Tetsuto Minami. Cueing the Necker cube: Pupil dilation reflects the viewing-from-above constraint in bistable perception. *Journal of Vision*, 20(4), 7-7, 2020.

3.1 Introduction

Our visual system receives two-dimensional information from each image on the retina. From these two-dimensional images, it restores to vision the three-dimensional shape of the object, sometimes resolving ambiguities in the visual input in an automatic and unconscious manner. As a way of resolving perceptual ambiguity, Nakayama and Shimojo (1992) proposed a theoretical framework in which the visual system tends to interpret images and surfaces as seen from a generic point, instead of an accidental vantage point [60]. In other words, the object properties of ambiguous images are estimated based on constraints derived from past visual experiences.

Several visual generic principles have been proposed for disambiguating the perception of objects (e.g., the light-from-above constraint; [61]). The view-from-above (VFA) constraint or heuristic is a bias in vision so that whenever the input information is ambiguous and consistent with different viewpoints on the same object [62], the VFA is preferred in perception over the alternative view-from-below.

Kornmeier and colleagues suggested that observers prefer the VFA due to an asymmetry of perceptual experiences or statistical learning, according to which we more often look down on objects (e.g., artifacts) than look up at them [63]. Remarkably, Sundareswara and Schrater (2008) showed that the VFA preference of Necker cubes is close to 100% for concise presentations and declines for long exposures, but it remains the most likely interpretation. As these authors pointed out, in Bayesian models of perception, the visual system tends to choose the optimal interpretation among alternatives, typically the viewpoint with maximal posterior probability [64]. Hence, a Bayesian account suggests that VFA may be the most frequent experience with many types of common objects, which are usually manipulated at the hand level, and therefore examined from a top view. Supposedly, the Necker cube may be spontaneously interpreted as a representation of some kind of smaller-than-the-body box that could be “afforded” by the hands.

Toppino (2003) suggested that the top-down activation or priming of perceptual representations affects a specific interpretation of the cube in the Necker cube. Some studies showed that one could control to some extent the perception of an ambiguous figure by focusing on spe-

cific portions of the figure, or by intentionally selecting appropriate focal features by using the Necker cube [78] or the so-called “my husband and my father-in-law” drawings [79]. Wernery, Atmanspacher, and Kornmeier (2015) showed that the dwell time (i.e., periods of transiently stable percepts), while passively observing the Necker cube for 3 minutes, was longer for the VFA than the one from below [80]. Importantly, Meng and Tong (2004) showed that selective attention can bias reversals of the perception of the Necker cube [81].

Despite many studies on the VFA bias, most of these are psychophysical experiments in which the introspective reports of participants are the dependent variable. I reason that evidence for a VFA bias can also be revealed independently by using a physiological index. I specifically focused on the method of pupillometry, which has been previously used to investigate bistable perception [59]. A pupillary dilation temporally close to a reversal in perspective of the Necker cube has been interpreted as a physiological signal of a “reset” mode in consciousness [82], driven by noradrenergic activity in the brain. In the present study, I use pupillometry as an index of the intensity of cognitive processing or of attention, as originally suggested by Kahneman (1973), Hess and Polt (1964), Kahneman and Beatty (1966), and Just and Carpenter (1993) [83–86]. Specifically, I hypothesized that if one perspective of the two (above/below) has been more frequent in past encounters with similar objects, then one view-specific memory should be less effortful or more “fluent” than the other.

Several previous studies have investigated voluntary control in bistable stimuli [63, 87–89], suggesting that the rate of perceptual switching is modulated by voluntary control, which seems consistent with our present results. For example, eye movements and eye position can affect perceptual switching, including eye movements or saccades [88, 90] and eye position [91]. In this study, I designed an experimental paradigm that avoids the influence of eye gaze positions by requesting participants to maintain central fixation during stimulus presentation.

Specifically, priming one particular surface of the Necker cube by briefly making it opaque at the start of a trial should be more effective in disambiguating the view of the cube whenever the cued surface is consistent with a VFA than when consistent with a view-from-below (see Figure 3.1). Moreover, I predicted that when cueing a surface consistent with a view-from-below, reversals to the alternative view should be more frequently reported than when cueing a surface

consistent with a VFA. In all of the earlier described cases, the less “fluent” perspective should be indexed by a larger size of the pupil (cf. Yoshimoto, Imai, Kashino, & Takeuchi, 2014 [92]) consistent with increased cognitive workload or in intensive attention [83].

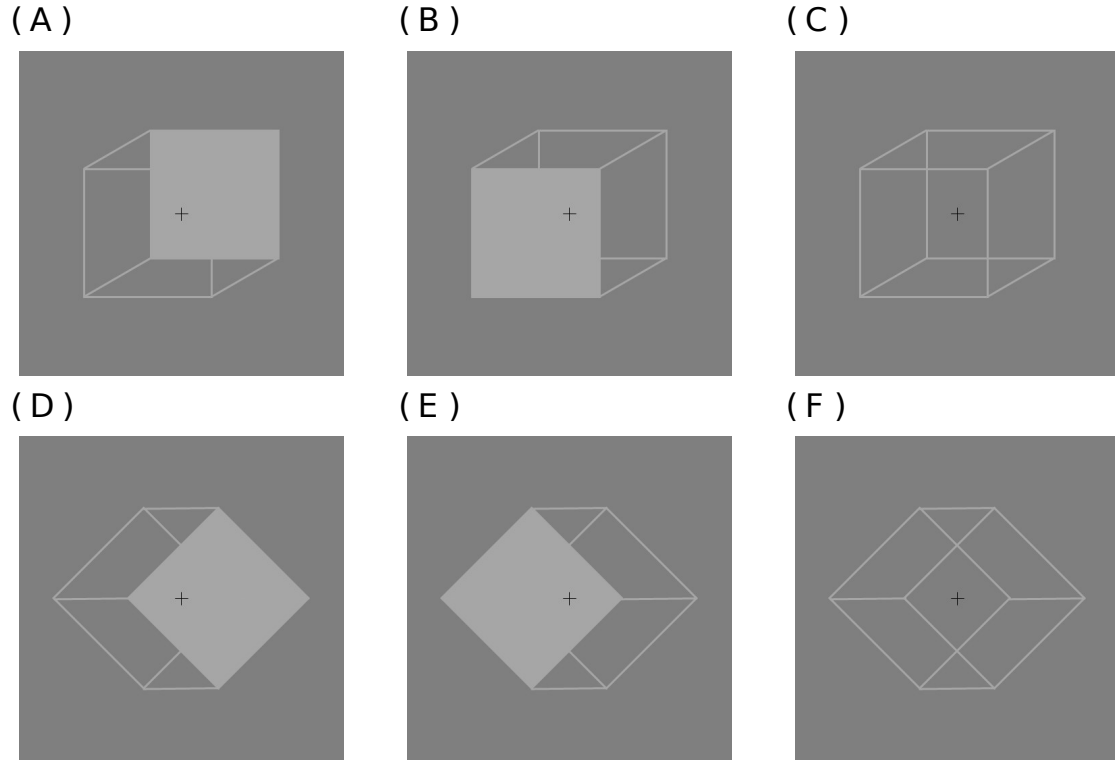


Fig. 3.1: Stimuli used in Experiment 1 and 2.

Stimuli used in Experiments 1 and 2 (top and bottom panels, respectively). Figures (A, B, D, and E) were used for priming. Figures (C and F) shows the standard Necker cube.

Finally, I hypothesize that maintaining the perception of a specific view may be more likely to reveal a VFA bias in the forced attention condition than during passive viewing of the Necker cube. I also note that in previous studies of perceptual switching with pupillometry, it has been debated whether perceptual switching causes pupil dilation and whether it may be simply triggered by the motor response [59, 93]. In this study, participants’ responses regarding the perspective of perception were collected after the offset of the stimuli; therefore the present paradigm can separate between the occurrence of a perceptual switch and the motor response

when reporting it.

3.2 Experiment 1

In the first experiment, I ascertained whether the pupil diameter can index reduced effort, as expected if there is a VFA bias, when viewing a bistable (Necker) cube. In each trial, either the top or bottom sides of the Necker cube was filled-in for 3 seconds with an opaque white hue. This was intended to cue attention toward the surface and consequently bias a specific perspective consistent with a front side position of the surface. Subsequently, the surface became transparent, and a classic (wireframe) Necker cube was shown for 3 seconds. In a passive viewing blocked condition, participants simply kept fixation on a cross-centered in the middle of the Necker cube. In the forced attention condition, the participants were asked to maintain in their perception the perspective that had been initially cued, while also keeping central fixation (see Figure 3.2).

I reasoned that maintaining a VFA perspective should require fewer attentional resources than a view-from-below perspective, particularly so when engaging top-down intensive attention in the forced attention condition. Therefore I expected a difference in pupil diameter after cueing either the top or bottom side of the Necker cube, and particularly so in the attention condition.

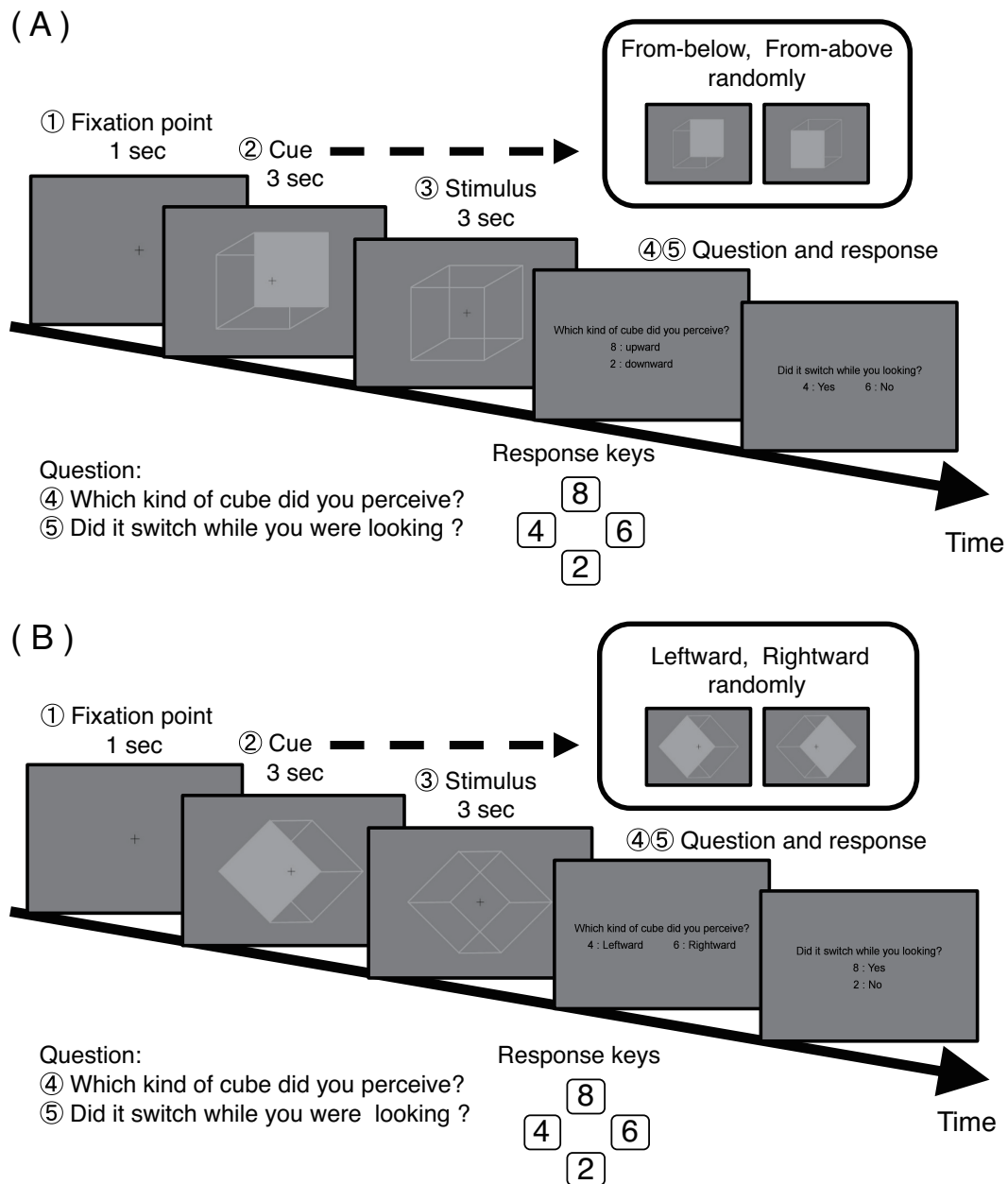


Fig. 3.2: Timeline of Experiment 1 and 2.

(A) Timeline of Experiment 1. The arrow shows the sequence of images presented to participants with the corresponding presentation times. Participants answered two questions after stimuli presentation: (1) “Which kind of cube did you perceive?” and (2) “Did it switch while you were looking?” The former question was answered by pressing “8” as “upward” and “2” as “downward” by Two-alternative forced-choice (2AFC). “Upward” refers to the appearance of viewing from below, and “downward” refers to viewing-from-below. The inset above illustrates the two possible cues. In the passive viewing condition, participants simply looked at a fixation cross on the Necker cube. In the forced attention condition, the participants were asked to maintain the same perspective as the one initially cued, while also keeping fixated on the central cross. (B) Experimental procedure in Experiment 2. Same as in the above panel except for the rotated Necker cube stimuli. Questionnaire sentences were also the same, but the former was answered by pressing “4” as “leftward” and “6” as “rightward,” and the latter was answered by pressing “8” as “yes” and “2” as “no.”

3.2.1 Materials and methods

Participants

Twenty-eight healthy subjects participated in Experiment 1. Four participants were excluded from pupil analyses because two participants had eye blinks on more than 70% of the trials, one participant misunderstood the instructions of the tasks, and one participant never shifted perception to another perspective, yielding a final study group size of 24 participants (mean age, 23.00 years; SD, 1.56; 4 women).

All participants self-reported that they had a normal or corrected-to-normal visual acuity. The experimental procedures received approval from the Committee for Human Research at the Toyohashi University of Technology. Participants provided written informed consent, and the experiment was conducted in accordance with the guidelines of the committee.

To ensure adequate statistical power = 0.8 ($1 - \beta$ the probability that the test rejects the null hypothesis when a specific alternative hypothesis is true), the sample size was a priori determined by a power analysis based on predicted effect size using G*Power version 3.1.9.2 [94]. Thus the present study's sample size was above the estimated sample size range of $N = 24$ necessary to find large-to-medium effects in a repeated-measures analysis of variance (ANOVA), given the error probability of $\alpha = 0.05$ (effect size estimates for each main effect and interaction are given later by partial eta-square(η^2) for ANOVA) [95].

Stimuli and apparatus

I used three kinds of images in Experiment 1. Two images were unambiguous figures of cubes generated by shading one surface of the Necker cube drawing (Figures 3.1A and B). The third image was the standard Necker (wireframe) cube (Figure reffig:1C). The cube occupied 7.7° horizontally and 7.7° vertically in visual angle. The color of the cube edges was light gray (78.8 cd/m^2) on a gray background (60.9 cd/m^2). The fixation cross was black (0.4 cd/m^2) with a $0.9^\circ \times 0.9^\circ$ size in visual angle. These images were created first with Microsoft PowerPoint

2016 (Microsoft Corp., Redmond, WA) and adjusted with MATLAB (MathWorks, Natick, MA) using Psychtoolbox 3.0 [69]. All stimuli were shown on an LCD display (Display++, Cambridge Research Systems, Kent, United Kingdom) at a refresh rate of 120 Hz.

Procedure

Figure 3.2(A) shows the timeline of one trial in Experiment1. First, the fixation cross was shown for 1000 ms, and then a cube with either the top or bottom side rendered opaque was presented for 3000 ms as a cue (hereafter called “cue”). Two kinds of images were used randomly as cues: one yielded the perspective of a cube seen from above and the other the perspective from below. After the cue, the standard Necker cube was shown (by removing the surface shading while leaving the standard wireframe) for 3000 ms, and at its offset the participants reported (by pressing one of two forced-choice keys) which percept they saw initially and whether a reversal to the alternative perspective occurred while viewing the empty cube. The experiment consisted of two conditions (passive viewing and forced attention), each with 40 trials (each cue type \times 20 trials). The order between the two conditions was counterbalanced by inverting it for every other participant. In the passive viewing condition, participants simply looked at a fixation cross on the Necker cube. In the forced attention condition, the participants were asked to maintain the same perspective as the one initially cued, while also keeping fixated on the central cross. Participants were also instructed to refrain from blinking as much as possible during each trial.

3.2.2 Recording and Analysis

Behavioral Analysis

From the participants’ key-press responses, I calculated the probability that they perceived the same appearance as primed by the cue. The probability of a percept was obtained by dividing the number of trials in which the participant’s initial percept was congruent with the cued appearance by all of the trials in each condition (20 trials). Similarly, I calculated the probability that the participant’s percept switched while viewing the empty Necker cube. This was obtained by dividing the number of trials in which a participant’s percept switched by all the trials in the condition (20 trials). For statistical analysis, a two-way repeated-measures ANOVA

was performed with perspective (from above, from below) and attention (passive, forced) as the within-subject factors in these probabilities. Pairwise comparisons for main effects in the ANOVA were corrected for multiple comparisons using the Bonferroni method. In addition, to investigate the effect of the cue, the number of trials of all participants who perceived the same appearance of the cue was calculated, and binomial tests were performed in each condition. The level of statistical significance was set to $p < 0.05$ for all analyses.

Pupil recording and analysis

Pupil sizes and eye movements were measured during the task by a noninvasive infrared eye tracker (iViewX RED500, SensoMotoric Instruments, Teltow, Germany) at a sampling rate of 500 Hz. Eye movements were monitored from both eyes. The positions of both eyes were acquired by nine-point calibration at the start of the experiment. For analyses, we averaged the pupil diameters from both eyes. Trials in which the pupil could not be detected were excluded from the analysis. Pupil recordings were smoothed using a sliding average (80-ms time window). In the time-course analysis, each trial was normalized by subtracting pupil size at stimulus onset from the baseline pupil size. Baseline pupil size was computed as an average of data collected – 500 ms prior to stimulus onset (0 ms). I calculated the time course of the trial's average pupils when the participants perceived either the upward cube (view-from-below) or the downward cube (VFA) in correspondence with the perspective primed by the cue. In the time course of pupil diameter changes, the significant differences were corrected with a false discovery rate for multiple comparisons using the Benjamini and Hochberg method [96]. Specifically, the average pupil diameters from 220 to 3000 ms after stimulus presentation were calculated, and a repeated-measures ANOVA was performed to assess the presence of significant differences in pupil diameter, with perspective (from above, from below) and attention (passive, forced) as the within-subject factors. The reason for excluding data before 220 ms is based on the known latency of the light reflex, which has a minimum of approximately 220 ms [97]. Furthermore, to separate the effects of perceptual perspective and perceptual switching, I extracted and analyzed only those trials in which there occurred no perceptual switching. This additional ANOVA was also performed with perspective and attention as factors. Finally, I calculated the averaged time course of pupil diameter in separate trials in which a perceptual switching occurred or was absent to better reveal how perceptual switching per se affected pupil diameter in each

attentional condition. Pairwise comparisons for main effects in the ANOVA were corrected for multiple comparisons using the Bonferroni method, and the level of statistical significance was set at $p < 0.05$ for all analyses as for the behavioral analysis.

3.2.3 Results

Behavioral Results

I computed the participants' key presses indicating their subjective view during perception. Based on the earlier described data, I found that the probability to perceive the Necker cube as having the same perspective as primed by the cue was greater in the forced attention condition than in the passive viewing condition (see Figure 3.3(A)). In addition, the probability of a from-below appearance was lower than that from-above. The ANOVA revealed a main effect of Attention [$F_{(1,23)} = 28.46$, $p < 0.001$, $\eta_p^2 = 0.55$] and Perspective [$F_{(1,23)} = 8.91$, $p = 0.007$, $\eta_p^2 = 0.28$]. There was no significant interaction between Attention \times Perspective [$F_{(1,23)} = 0.10$, $p = 0.76$, $\eta_p^2 = 0.004$].

Next, I also calculated the perceptual switching probabilities. An ANOVA on the switches showed an attention by perspective interaction, $F_{(1,23)} = 12.38$, $p = 0.002$, $\eta_p^2 = 0.35$. To identify more detailed effect of the factors, a post hoc test revealed a simple effect in the forced attention condition, $F_{(1,23)} = 4.88$, $p = 0.04$, $\eta_p^2 = 0.18$, indicated that the perceptual switching probability toward a from-above perspective was higher than toward a view-from-below. In addition, a post hoc test revealed a simple effect in the from-below perception, indicating that the perceptual switching probability of forced attention condition was lower than in the passive condition $F_{(1,23)} = 8.55$, $p = 0.008$, $\eta_p^2 = 0.27$. There was no main effect of attention [$F_{(1,23)} = 1.62$, $p = 0.22$, $\eta_p^2 = 0.27$] and perspective $F_{(1,23)} = 1.16$, $p = 0.29$, $\eta_p^2 = 0.05$].

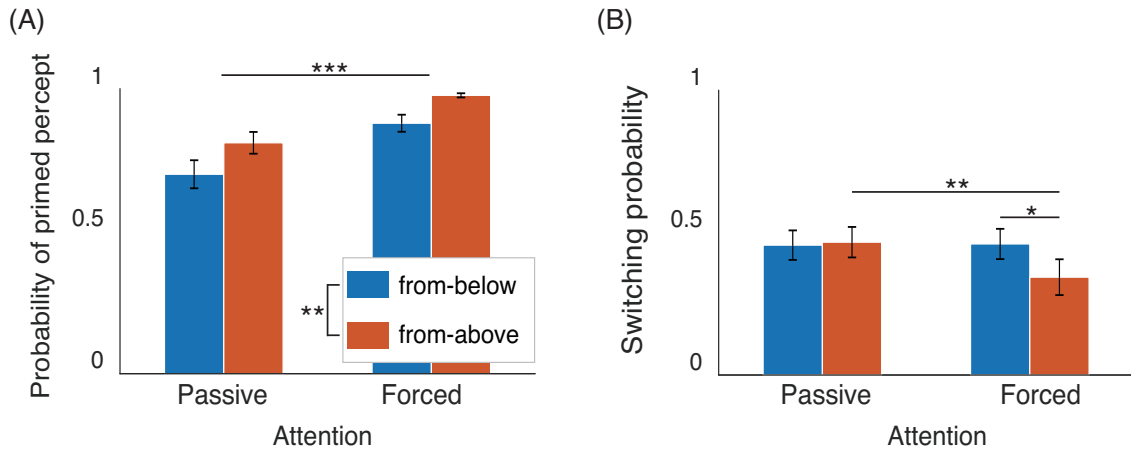


Fig. 3.3: Behavioral results in Experiment 1.

Bar graphs (A) show grand average probability of the participants perceived the same appearance as the cue. (B) Grand average of switching probability during stimulus presentation. Both results are in Experiment 1. Asterisks on horizontal lines represent a significant difference (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Pupillometry Results

Time course of pupils when perceiving either the view-from-below or VFA

Time course of the pupils when participants perceived either the view-from-below or VFA: I then analyzed the time course of the pupil diameter to confirm a relationship of pupil size for the perceived perspectives between the attentional conditions. These analyses were conducted for trials in which the perception was congruent with the prior cue because the number of trials in which perception was incongruent with the prior was too small (i.e., the grand average probability of incongruent perception in all condition and all participants was 15.8%; see Figure 3.3A). Figures 3.4A and B showed the grand-averaged time course of changes in pupil diameter when the participants perceived the view-from-below the cube or from above the cube during the stimulus presentation for 3 seconds in passive viewing and forced attention condition, respectively. An ANOVA was carried out to compare the mean pupil dilation from 220 to 3000 ms in the two attention and perspective conditions (Figure 3.4C). There was, however, no significant main effect of attention, $F_{(1,23)} = 0.09$, $p = 0.76$, $\eta_p^2 = 0.004$ nor a main effect of perspective, $F_{(1,23)} = 2.47$, $p = 0.13$, $\eta_p^2 = 0.01$. There was also no evidence for an interaction between attention and perspective $F_{(1,23)} = 2.71$, $p = 0.11$, $\eta_p^2 = 0.10$.

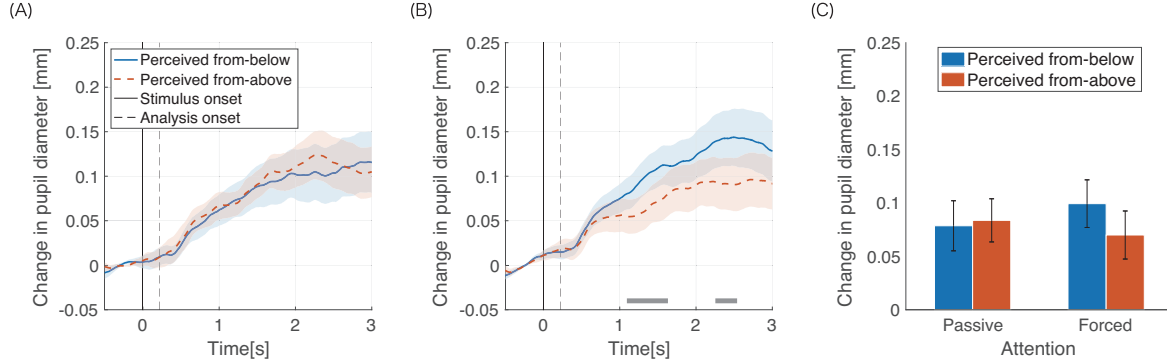


Fig. 3.4: Pupillometry results classified by perceived perspectives in Experiment 1.

(A) Passive viewing condition: grand-averaged time course of pupil changes during the presentation time of 3 seconds. The horizontal axis indicates the time (in seconds), and the vertical axis indicates pupil dilation (in mm) relative to baseline (from -500 to 0 ms). Shaded colors are the standard error of the mean. (B) Forced attention condition: grand-averaged time course of pupil changes during presentation time for 3 seconds. The gray horizontal bars in the middle panel represent significant differences between the perspective condition of view-from-above and from-below trials; p values were corrected for multiple comparisons with an expected False Discovery Rate (FDR) of 0.05. (C) Bars show the mean pupil dilation from 220 to 3000 ms in the attention condition and perspective condition, respectively.

Trials with no perceptual switching

The previous analysis included only trials with perceptual switching during the stimulus presentations. Thus the previous analysis results included not only the effect of perceptual switching but also the effect of different perceptual appearances after perceptual reversal. In the present analysis, I excluded switch trials so as to examine in detail the effect of a specific view. Two participants for which no perceptual switching occurred under any one of the conditions were rejected from the analysis. Figures 5 (A and B) shows the grand-averaged time course of the changes in pupil diameter when the participants perceived either the upward cube (view-from-below) or the downward cube (VFA) with the condition of nonswitching trials during the stimulus presentation for 3 seconds in passive viewing and forced attention condition, respectively. Importantly, as seen in an ANOVA, there was a significant interaction of attention \times perspective, $F_{(1,21)} = 5.06$, $p = 0.035$, $\eta_p^2 = 0.19$ (see Figure 5C). A post hoc test revealed that the pupil diameter was significantly larger for the perspective from below than from above in

the condition of forced attention, $F_{(1,21)} = 7.44$, $p = 0.013$, $\eta_p^2 = 0.26$. There were no significant main effects for either attention, $F_{(1,21)} = 0.19$, $p = 0.66$, $\eta_p^2 = 0.009$, or perspective, $F_{(1,21)} = 1.62$, $p = 0.22$, $\eta_p^2 = 0.07$.

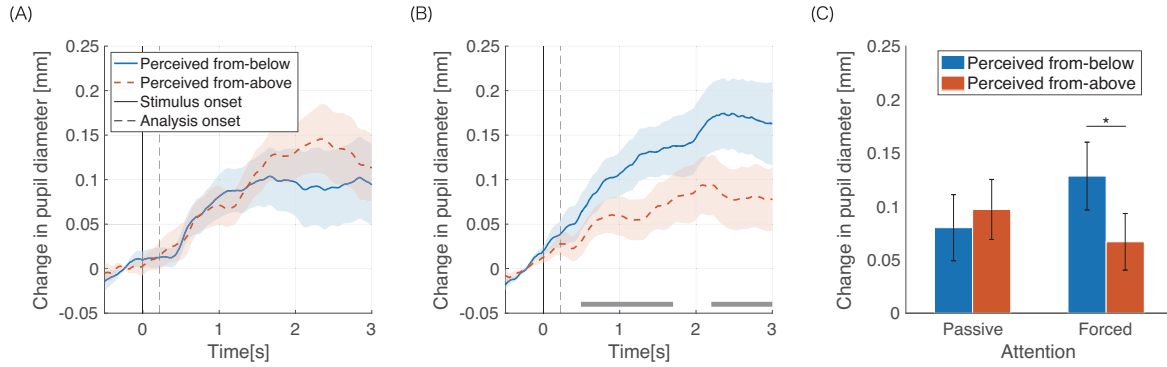


Fig. 3.5: Pupillometry results classified by perceived perspectives during nonswitch trials in Experiment 1.

(A) Passive viewing condition: grand-averaged time course of pupil changes during presentation time for 3 seconds. The horizontal axis indicates the time (in seconds), and the vertical axis indicates pupil dilation (in mm) relative to baseline (from -500 to 0 ms). Shaded colors indicate the standard error of the mean. (B) Forced attention condition: grand-averaged time course of pupil changes during presentation time for 3 seconds. Shaded colors indicate the standard error of the mean. The gray horizontal bars in the middle panel represent significant differences between the perspective condition of view-from-above and from-below trials; p values were corrected for multiple comparisons with an expected False Discovery Rate (FDR) of 0.05 (C). Bars show the mean pupil dilation from 220 to 3000 ms in attention condition and perspective condition, respectively. Asterisk represents a significant difference ($*p < 0.05$). The result shows that there was a significant difference in the amount of change in pupil diameter between perceived from below and from above with forced attention condition, even though there was no button response no perceptual switching.

Time course of the pupils during nonswitch versus switch trials

To investigate whether the pupils were dilated due to perceptual switching, I calculated time courses separately for the nonswitch and switch trials. Figure 6 shows the averaged time courses of pupil diameter when perceptual switching occurred or did not during passive viewing. The t -tests revealed no significant difference in the time sequence data.

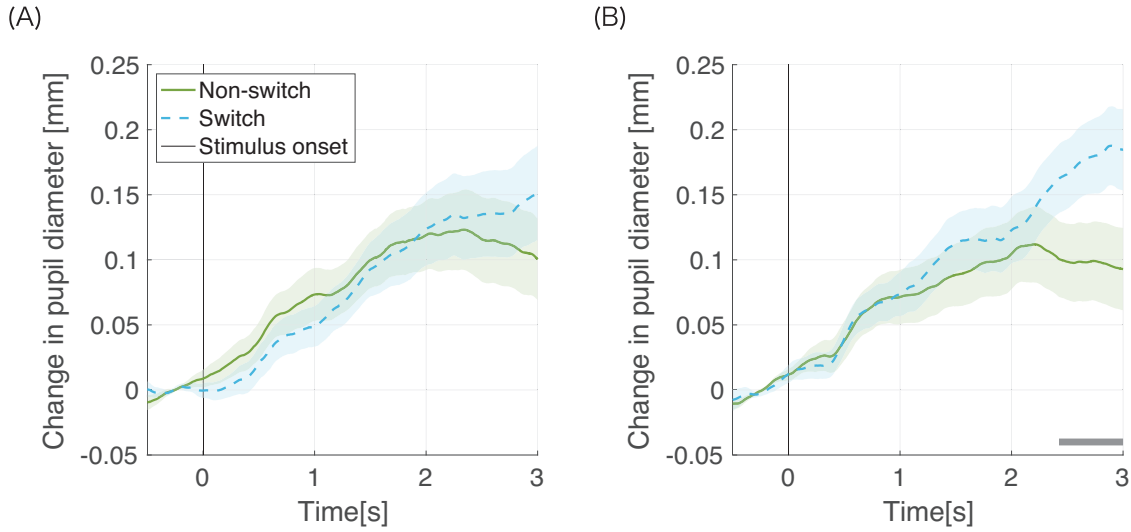


Fig. 3.6: Pupillometry results separating nonswitch trials versus switch trials in Experiment 1.

(A) Passive viewing condition: averaged time courses of pupil diameter separately for perceptual switching trials and nonswitching trials. (B) Forced attention condition: averaged time courses of pupil diameter separately for perceptual switching trials and nonswitching trials. Shaded colors indicate the standard error of the mean. The gray horizontal bar represents a significant difference between nonswitch trials and switch trials; p values were corrected for multiple comparisons with an expected False Discovery Rate (FDR) of 0.05. Please note that 0 seconds represents the onset of the ambiguous Necker stimuli.

3.2.4 Discussion

The present findings confirm that priming one specific view of the Necker cube was effective, and the shading cue preceding the presentation of the wireframe typically evokes the corresponding view. However, as expected, I observed a change in pupil diameter only when I instructed the participants to actively sustain a specific perspective.

3.3 Experiment 2

In Experiment 2, I further tested the idea that the ease in sustaining a particular perceptual interpretation of the bistable Necker drawing, and its effect on the pupil diameter, reflects an

ecological VFA constraint on internal representations or heuristic. I reasoned that, by rotating the stimuli used in the previous experiment of 90° , I would exclude the presence of any perspective bias because these particular views of the cube appear to be rare. As visible in Figure 3.1 (bottom panel), these rotated perspectives of the same Necker cube do not seem familiar, especially considering our real-world experience with solid cubes (i.e., a real cube in any of the two possible perspectives in the images would be gravitationally unstable because in both views the cube appears to be poised on the tip of one corner).

3.3.1 Materials and methods

Twenty-seven healthy subjects participated in Experiment 2. Two participants were excluded from pupil analyses because one showed eye blink in more than 70% of the trials, and one participant had difficulty performing the task, yielding a final study group size of twenty-five participants (21 men, four women; mean age, 22.76 years; SD, 1.64). All participants had a normal or corrected-to-normal visual acuity. Again, the experimental procedures received the approval of 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, and all participants provided written informed consent. The study's sample size was based, as explained previously, on an estimated sample size of $N = 24$.

Stimuli and apparatus

The apparatus was the same as in Experiment 1. Stimuli in Experiment 2 were also identical and simply rotated on the frontal plane.

Procedure

The procedure was identical to Experiment 1 (Figure 3.2(B)). Two types of stimuli were used randomly as cue: one was the perspective of a rightward (Figure 3.1(D)) cube and the other perspectives of leftward (Figure 3.1(E)). The only difference was that responses of "leftward" and "rightward" perspectives were used instead of "from-below" and "from-above".

3.3.2 Recording and Analysis

Behavioral Analysis

As done previously, I calculated the probability that participants perceived the same appearance as primed by the cue. For statistical analysis, a two-way repeated-measures ANOVA was performed with perspective (leftward, rightward) and attention (passive, forced) as within-subject factors. Binomial tests were also performed in each condition.

Pupil analysis

The analyses of the pupils were performed as previously by first calculating the grand-averaged time course of the average pupils when the participants perceived either the leftward or rightward in correspondence to the perspective primed by the cue. I calculated the average pupil diameters from 220 to 3000 ms after stimulus presentation, and an ANOVA was performed with perspective and attention as factors. Moreover, to separate the effects of perceptual perspective and perceptual switching, I analyzed only those trials in which there was no perceptual switching. Finally, I calculated the averaged time course of pupil diameter in trials in which perceptual switching occurred or was absent, so as to clarify how perceptual switching affected the pupil diameter in each attentional condition.

3.3.3 Results

Behavioral Results

The probability to perceive the same appearance of the cube as cued was greater in the forced attention condition than passive viewing condition (see Figure 3.7A). As shown by binomial tests, both attention and perspective were significantly different from 0.5 of a chance level ($p < 0.001$). In addition, the probability of leftward perception was lower than rightward. The ANOVA revealed a main effect of attention, $F_{(1,24)} = 17.81$, $p = 0.0003$, $\eta_p^2 = 0.43$, and perspective, $F_{(1,24)} = 7.20$, $p = 0.013$, $\eta_p^2 = 0.23$. There was no significant interaction between attention \times perspective, $F_{(1,24)} = 2.40$, $p = 0.13$, $\eta_p^2 = 0.09$.

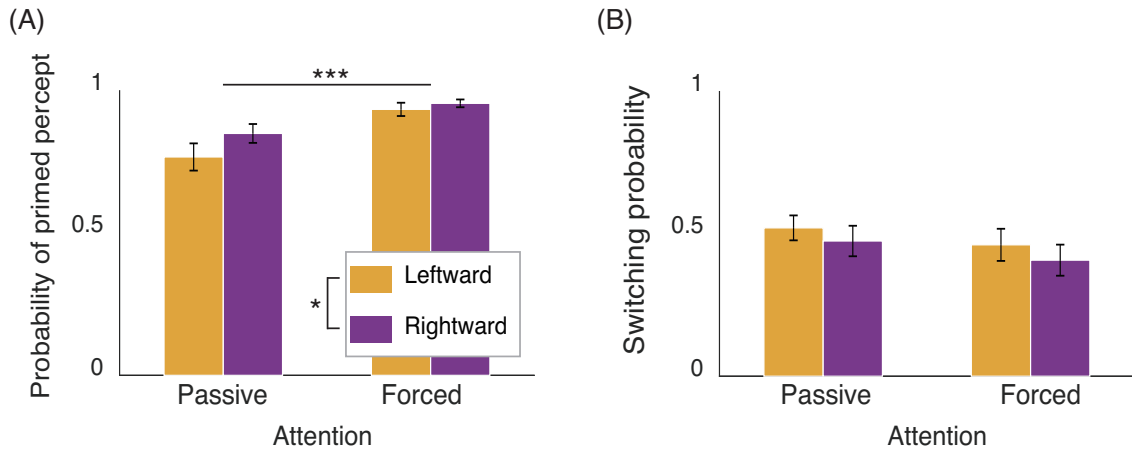


Fig. 3.7: Behavioral results in Experiment2.

(A) Grand average probability of the perceptions of the cued perspectives. (B) Grand average of switching probability. Both results are in Experiment 2. Asterisk represents a significant difference (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Figure 3.7(B) shows the result of perceptual switching probability. There was no significant main effect between either attentional conditions, $F_{(1,24)} = 1.43$, $p = 0.24$, $\eta_p^2 = 0.06$]or perspective, $F_{(1,24)} = 1.97$, $p = 0.17$, $\eta_p^2 = 0.08$, or their interaction, $F_{(1,24)} = 0.03$, $p = 0.87$, $\eta_p^2 = 0.01$.

Pupillometry Results

Time course of pupils when perceiving either the leftward cube or the rightward cube

I analyzed time courses of change in pupil diameter as done for Experiment 1. As expected, an ANOVA on average changes in pupil diameter from 220 to 3000 ms (Figure 3.8C) showed no significant difference in any main effect (main effect of attention: $F_{(1,24)} = 1.24$, $p = 0.28$, $\eta_p^2 = 0.05$; main effect of perspective: $F_{(1,24)} = 0.05$, $p = 0.83$, $\eta_p^2 = 0.002$, and the interaction between attention \times perspective missed the significant cutoff, $F_{(1,24)} = 0.24$, $p = 0.63$, $\eta_p^2 = 0.01$).

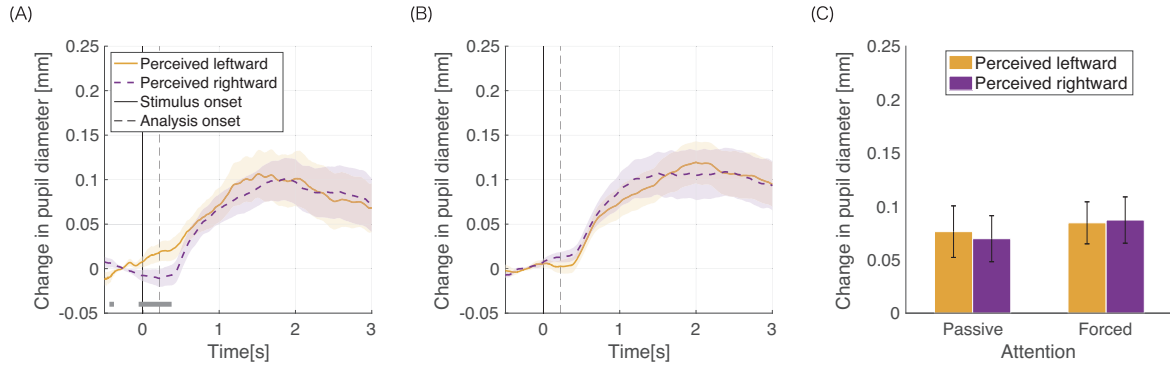


Fig. 3.8: Pupillometry results classified by perceived perspectives in Experiment 2.

(A) Passive viewing condition: grand-averaged time course of pupil changes during presentation time for 3 seconds. The horizontal axis indicates the time (in seconds) and the vertical axis indicates pupil dilation (in mm) relative to baseline (from -500 to 0 ms). Shaded colors indicate the standard error of the mean. The gray horizontal bar represents the significant difference between the perspective condition of leftward and rightward trials; p values were corrected for multiple comparisons with an expected False Discovery Rate (FDR) of 0.05 . (B) Forced attention condition: grand-averaged time course of pupil changes during presentation time for 3 seconds. Same conventions as A. (C) Bars show the mean pupil dilations from 220 to 3000 ms in the attention and perspective conditions.

Nonswitch trials

As done earlier, to reveal the effect of perspective, I further analyzed time courses of change in pupil diameter as in Experiment 1 (Figures 3.9A and B). I excluded five participants for which no perceptual switching occurred under any one of the conditions. An ANOVA showed no significant difference main effect (Figure 3.9C): attention: $F_{(1,19)} = 0.94$, $p = 0.34$, $\eta_p^2 = 0.047$; perspective: $F_{(1,19)} = 3.10$, $p = 0.094$, $\eta_p^2 = 0.14$. There was no interaction between attention \times perspective: $F_{(1,19)} = 0.02$, $p = 0.97$, $\eta_p^2 = 0.0001$ (see Figures 3.9A and B).

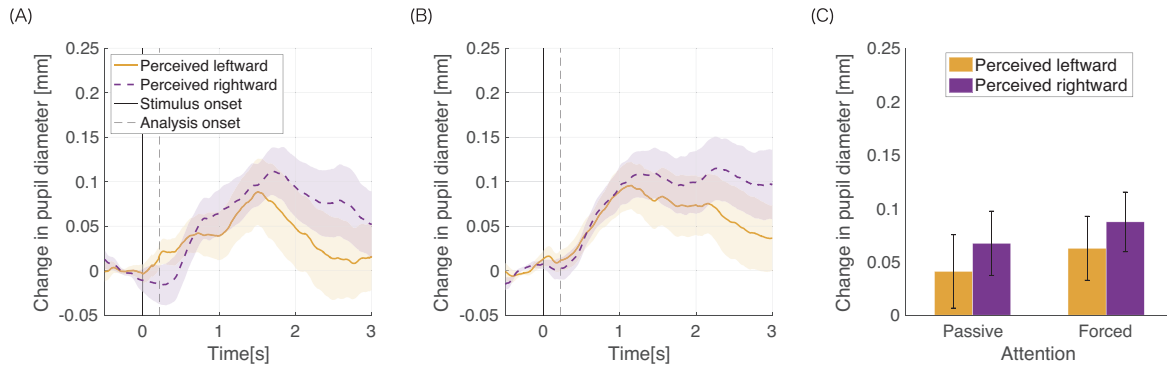


Fig. 3.9: Pupillometry results classified by perceived perspectives during nonswitch trials in Experiment 2.

(A) Passive viewing condition: grand-averaged time course of pupil changes during presentation time for 3 seconds. The horizontal axis indicates the time (in seconds) and the vertical axis indicates pupil dilation (in mm) relative to baseline (from -500 to 0 ms). Shaded colors are the standard error of the mean. (B) Forced attention condition: grand-averaged time course of pupil changes during presentation time for 3 seconds. Same conventions as A. (C) Bars show the mean pupil dilation from 220 to 3000 ms in attention condition and perspective condition.

Time course of pupils during and switch trials

Finally, I calculated time courses separately between the nonswitch and switch trials, as done in Experiment 1. Figure 10 shows the averaged time courses of pupil diameters when perceptual switching occurred or not in each of attentional condition.

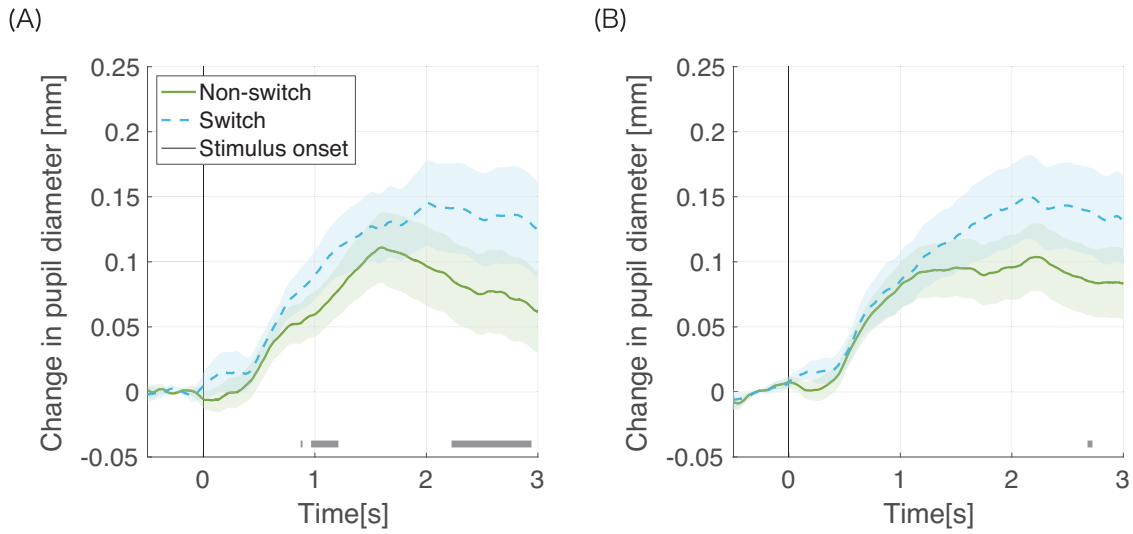


Fig. 3.10: Pupillometry results separating nonswitch trials versus switch trials in Experiment 2.

(A) Passive viewing condition: averaged time courses of pupil diameter separately for perceptual switching trials and nonswitching trials. (B) Forced attention condition: averaged time courses of pupil diameter separately for perceptual switching trials and nonswitching trials. Shaded colors indicate the standard error of the mean. The gray horizontal bar represents a significant difference between nonswitch trials and switch trials; p values were corrected for multiple comparisons with an expected False Discovery Rate (FDR) of 0.05. Please note that 0 seconds represents the onset of the ambiguous Necker stimuli.

3.3.4 Discussion

As expected, when the Necker cube drawings were rotated to physically unlikely positions, there was no indication of effort related to perspective, which is consistent with the absence of an ecological viewpoint constraint on these particular images. I found, however, confirmation of the effectiveness of forcing attention when sustaining a specific perceptual interpretation of the bistable figure. Interestingly, there was a slight preference for the rightward view of the cube. I surmise that, given that this view would correspond to a clockwise rotation of the VFA cued surface, there may be at work complex interaction between the VFA bias and spontaneous mental rotations to the more natural orientation of the stimuli. I speculate, considering that the right arm is stronger in most people [98], that most objects are naturally manipulated in a clockwise action when held and turned (e.g., caps and lids). I also note that there is some

evidence for a preference in “mentally rotating” abstract shapes in a clockwise direction (e.g., Koriatic & Norman, 1985 [99]; Liesefeld & Zimmer, 2011) [100].

3.4 General Discussion

I found that changes in pupil diameter were significantly larger when participants perceived the view-from-below than when they perceived the VFA of the Necker cube and, specifically, when actively attempting to maintain one of these perspectives. Moreover, the probability of maintaining a specific perspective in perception, after the disappearance of the cue, was greater during forced attention condition than in passive viewing. In addition, the probability of perceptual switching in the forced condition was lower than in the passive condition.

In a second experiment, we showed the same cubes after a 90° rotation, either leftward or rightward, yielding two equally unusual and physically unlikely perspectives (based on a gravitational constraint) of the bistable shape. Given that, in this case the alternative views do not differ in terms of an above or below viewpoint, I also expected to find no difference in pupil diameter. Indeed, whereas the views from above and below differed in terms of pupillary response, the views from left or right did not.

It is already known that eye movements and eye position can affect perceptual switching (e.g., eye movements: Toppino 2003 [88]; saccades: Van Dam & Van Ee 2006 [90]; eye positions: Einhäuser et al., 2004 [91]). In this study, I avoided the influence of eye gaze positions by requesting participants to maintain central fixation during stimulus presentation.

Several previous studies have also investigated voluntary control in bistable stimuli (e.g., Strüber & Stadler 1999 [87]; Toppino 2003 [88]; Van Ee, Van Dam, & Brouwer 2005 [89]; Kornmeier et al. 2009 [63]), suggesting that the rate of perceptual switching rate is modulated by voluntary control, which seems consistent with our present results.

Einhäuser and colleagues reported that pupil diameter increases around the time of a perceptual switching during perceptual rivalry [59]. However, another study reported that the degree

of pupil dilation does not predict subsequent stability in perceptual rivalry [93, 101]. Instead, a small (approximately 5% of change on average) but reliable pupil dilation was observed around the time of key presses, and 70% of pupil dilation could be accounted for by the motor response [93]. Another study also showed that a key press can influence both brain activity and pupil diameter [48]. In the present study, all key-press responses were performed after stimulus offset.

When I separated in the analyses trials with and without a switch, no statistically significant difference was found. Also, it seems likely that the observed differences in pupillary responses in our study reflected a difference in specific perceptual content (e.g., from-below appearance, from-above appearance) instead of effects of motor responses, as also suggested by Kloosterman and colleagues (2015) [102]. I also note that the interactive effect of attention and perspective remained significant in Experiment 1, even after excluding all trials in which a perceptual switch occurred.

In line with Kahneman's original account [83], I assume that pupil dilation reflects the allocation of attentional resources, and therefore that it provides an index of the level of mental effort exerted in a particular situation. I note that in this study, there was no significant pupil size difference between the two attentional conditions. However, attention affected the pupil diameter as an interactive effect because pupils were significantly dilated only when participants perceived the view-from-below than the VFA during forced attention condition. It seems reasonable to conclude that it is more effortful to actively sustain viewing-from-below than from above. Hence the VFA bias is reflected in the level of mental effort, that is, a reduced dilation of the pupil.

At the physiological level, pupil dilations that are related to cognitive processing are thought to result from an inhibitory effect on the parasympathetic oculomotor complex by release of norepinephrine (NE) from the locus coeruleus [103]. The LC sends its noradrenergic projections to virtually all brain regions (except the basal ganglia), with particularly dense projections to areas known to be important in attentional processing, such as the parietal cortex, the pulvinar nucleus of the thalamus, and the superior colliculus [104–106]. Single-cell recordings in monkeys [107, 108] and pharmacologic studies in humans [109, 110] have confirmed a physiological

link between the activity of the LC-NE system and changes in pupillary diameter, allowing the use of pupillometry to tap task-related changes in attentional states mediated by LC-NE activity [82,111]. Thus our results are consistent with the idea that the modulation of pupil diameter reflects top-down attentional processing and different levels of mental effort.

Another consideration can be based on the Bayesian theory of human perception [112,113], in which biases in perception toward specific interpretations, especially of ambiguous stimuli, tend to match the natural statistics of the environment [114–118]. Thus, in light of this account, the VFA bias during perception of the Necker stimulus should reflect the supposed higher frequency in adopting the from-above perspectives than from-below perspectives in everyday situations. Such a priori perceptual bias can thus be interpreted as a strong influence on long-term perceptual memory of repeated instances of disambiguation of sensory information [119]. Thus under the present task, a difference in the probability of memory retrieval from long-term memory will reflect a VFA bias and in turn the amount of attentional load that is mirrored in the pupil. Our results seem to support the earlier described interpretation because the VFA bias per se did not affect the pupil unless attention was forced to maintain a specific perspective.

3.5 Conclusion

To our knowledge, this is the first study to investigate whether the VFA bias influences effort, as expressed in pupil diameter when maintaining a specific percept. Because VFA may be the most frequent experience with many types of common objects, attending and maintaining this specific perspective requires a lower degree of mental effort.

Chapter 4

The bias of ambiguous figure and posture

A similar version of this chapter is in preparation to publish as:

Fumiaki Sato, Ryoya Shiimoto, Shigeki Nakauchi, and Tetsuto Minami. Backward and forward neck tilt affects perceptual bias when interpreting ambiguous figures. *Scientific Reports* 12, 7276 (2022).

4.1 Introduction

Visual information is inputted from the retina in the eyes. Thereafter, it is decoded, estimated, and constructed by the brain. Since it is computationally impossible to restore 3-dimensional (3D) information from 2-dimensional (2D) information, many previous studies have investigated the visual mechanism by which a 3D visual experience can be obtained from a 2D image of the retina. A well-known early study by Helmholtz has proposed “unconscious inference,” suggesting that vision is constructed by both the information received via the retina and the observer’s unconscious reasoning [120]. As it stands, numerous researchers have proposed visual heuristics for 2D estimation (e.g., light source estimation: When convex-concave ambiguity occurs, it is assumed that the light source is above [121](strictly, it may be biased to the left or right instead of directly above); the generic view principle: The visual system works as if it were viewing from a general viewpoint rather than accidental viewpoints [60]; and finally, the viewing-from-above bias: When ambiguous figures such as Necker cube is observed, the observer tends to choose a viewpoint from above rather than from below [62](see also a review [122]).

Although many studies have suggested the effect of perceptual heuristics, most of them investigated this by presenting the stimulus in front. Specifically, observers in many experiments encountered the stimulus by sitting on a seat and looking directly in front of them. Therefore, the relationship between posture and perceptual heuristics is unclear, and it remains unknown if the heuristics that accompany physical changes (i.e., posture changes) affect perception. I hypothesized that the visual content of perception changes depending on neck posture.

Classically, Gibson, who advocated for ecological psychology, recommended considering perception both for the stimuli and the environment [123]. If the general view is implicitly defined in the observer, as in the idea of the generic view principle, the perceived experience and its principle when looking up and down should be different. For example, in our daily life, it is easy to perceive the sun and light sources when facing up, and the ground when facing down. Previous studies suggest that recognizing the ground affects the perception of the size of distant objects [124]. Thus, such different upper and lower perceptual experiences were assumed to be associated with posture changes.

The relationship between posture and perception has been investigated in several studies, which have shown that size [125], apparent size, and brightness [126] vary depending on the position (or orientation) of the head. These phenomena are explained by proprioceptive theory, which proposes that the size and brightness of an object is learned in a natural environment; thus, an abnormal posture causes misestimation. In addition, studies have also investigated the relationship between head orientation and depth estimation [127,128]. However, how perceptual bias and the experiential context of perception affect their perception remains unclear.

To investigate this effect, I focused on the Necker cube, which is an ambiguous figure. The Necker cube can be perceived as having two appearances—one from above and one below. Further, the perceived probability of the changes in appearance depend on priming [129], top-down intention [63], eye movement [90], and eye position [91]. Moreover, the probability of initial perception has been shown to be greater when an object’s appearance is perceived from above than from below and reflects the viewing-from-above bias [64]. Taken together, perceived probability changes due to various factors. In this study, I hypothesized that such changes in probability caused by perceptual bias are also dependent on posture.

In a study with a similar purpose, participants’ behaviors were shown to affect perceptual bias [130]. This study that used a stimulus of a structure-from-motion cylinder, which may be perceived as rotating either clockwise (CW) or counterclockwise (CCW), investigated how participants’ behavior affected perception. The results suggested that perception was formed by linking visual input and motor function, which may be related to the sensorimotor system. However, in this experiment, the action input occurred concurrently with the visual input. Therefore, the following question remains: How is perceptual bias modulated by simply changing posture without action input?

I devised a paradigm that presents the Necker cube in 3D space using a head-mounted display to address this issue. I set the state at which the face is facing in front at 0 degrees and measured the perceptual probability and the pupil diameter when facing five different angles (-60, -30, 0, 30, and 60 degrees), vertically and horizontally. Pupillometry was used, as the pupil diameter is known to reflect a cognitive factor [82] and can estimate the perceptual state when seeing the Necker cube [131]. Therefore, the pupil index was used to test whether the changes in perceptual

probability accompanying changes in posture could be tracked. In addition, I applied the cueing paradigm to test whether prior information affected perception differently depending on neck posture [131]. Therefore, this study aimed to clarify the relationship between neck posture and visual heuristics from the aspects of both behavioral response and pupil diameter, an established physiological cognitive index.

4.2 Materials and Methods

4.2.1 Participants

Twenty-five healthy participants participated in Experiment 1 (mean age = 21.84 years, SD = 1.03; 24 men, 1 woman). One participant who could not provide data due to mechanical problems and one participant who misunderstood the instruction of the behavioral task were excluded from the data of Experiment 1; thus, 23 responses were obtained for the final analytic sample. In Experiment 2, 19 healthy participants participated (mean age = 22.3 years, SD = 1.05; 19 men). To estimate the sample size of the participants, a-priori power analysis was performed using PANGAEA [132] (Power ANalysis for GEneral Anova designs; see also www.jakewestfall.org/pangea). Assuming a medium effect size (Effect size (d) = 0.45), α = 0.05 and β (statistical power) = 0.95 was set. In the design of Experiment 1, I was interested in both 3-way and 2-way interactions, hence, I calculated the number of participants with statistical powers above 0.95 in both cases. In the design of Experiment 2, the number of participants was computed fixed to a second-order interaction. According to the calculations, the number of participants was estimated to be 22 participants in Experiment 1 and 23 participants in Experiment 2. These sample sizes are considered reasonable because they are close to the previous study investigating perceptual bias of Necker cube using pupillometry [131]. I recruited students from the university based on the estimated sample size. In Experiment 2, the number of applicants did not reach the target sample size, therefore, post-hoc analysis was performed. The statistical power was 0.99 based on the effect size of the result of Experiment 2 and the number of the participants. In both experiments, the male-female ratio of the subjects was biased, but since gender would not play a role in the illusory effect and/or pupil response, I recruited participants as they came. It was by chance that I had an over-representation of men. (It seems

to be a normal number considering that the male-female ratio at the university population is 9:1). The experimental procedures received approval from the Committee for Human Research at the Toyohashi University of Technology. Participants provided written informed consent, and the experiment was conducted in accordance with the guidelines of the committee.

Stimuli and apparatus

I used three kinds of images in Experiment 1, all of which were generated based on a previous study [64]. The first image was a wireframe drawn Necker cube (Figure 4.1a). The second and third images were unambiguous cubes, one as viewed from above (VFA) (Figure 4.1b) and the other as viewed from below (VFB; Figure 4.1c). The color of the cube edges were white (R, G, B = 255, 255, 255) on a grey background (R, G, B = 128, 128, 128). These Necker cubes were placed in the virtual reality (VR) space at a distance of 100 Unit with a size of 4×4 Unit (“Unit” is an arbitrary unit representing the length in the Unity environment: 1 Unit is approximately 1 m) and the visual angle was $2.29^\circ \times 2.29^\circ$. The fixation cross was black (R, G, B = 0, 0, 0) with a 1.15×1.15 size in visual angle. These images were first created with GIMP and adjusted with Unity.

In Experiment 2, I used the Necker cube and three background contexts (Figures 4.1a and 4.1c). One was a context that simulated the appearance from above (Figure 4.1c Top), and the second was a simulation that simulated the appearance from below (Figure 4.1c Middle). These two were flipped upside down and had the same brightness. The third background context was a grey-filled cube with no upper and lower cue created by Matlab (Figure 1c Bottom). The average luminance of these stimuli were 37.61 cd/m². The Necker cubes were placed in the VR space at a distance of 100 Unit with a size of 2×2 Unit, and the visual angle was 1.15×1.15. These contents were placed in the VR space at a distance of 100 Unit with a size of 12×24 Unit, and the visual angle was 6.89×13.69.

All stimuli were shown on a Head Mount Display (HMD; HTC VIVE, HTC Corporation, Taiwan) at 2,160×1,200 pixels with a refresh rate of 90 Hz. An HTC VIVE controller (HTC VIVE, HTC Corporation, Taiwan) was used to obtain participants’ behavioral responses.

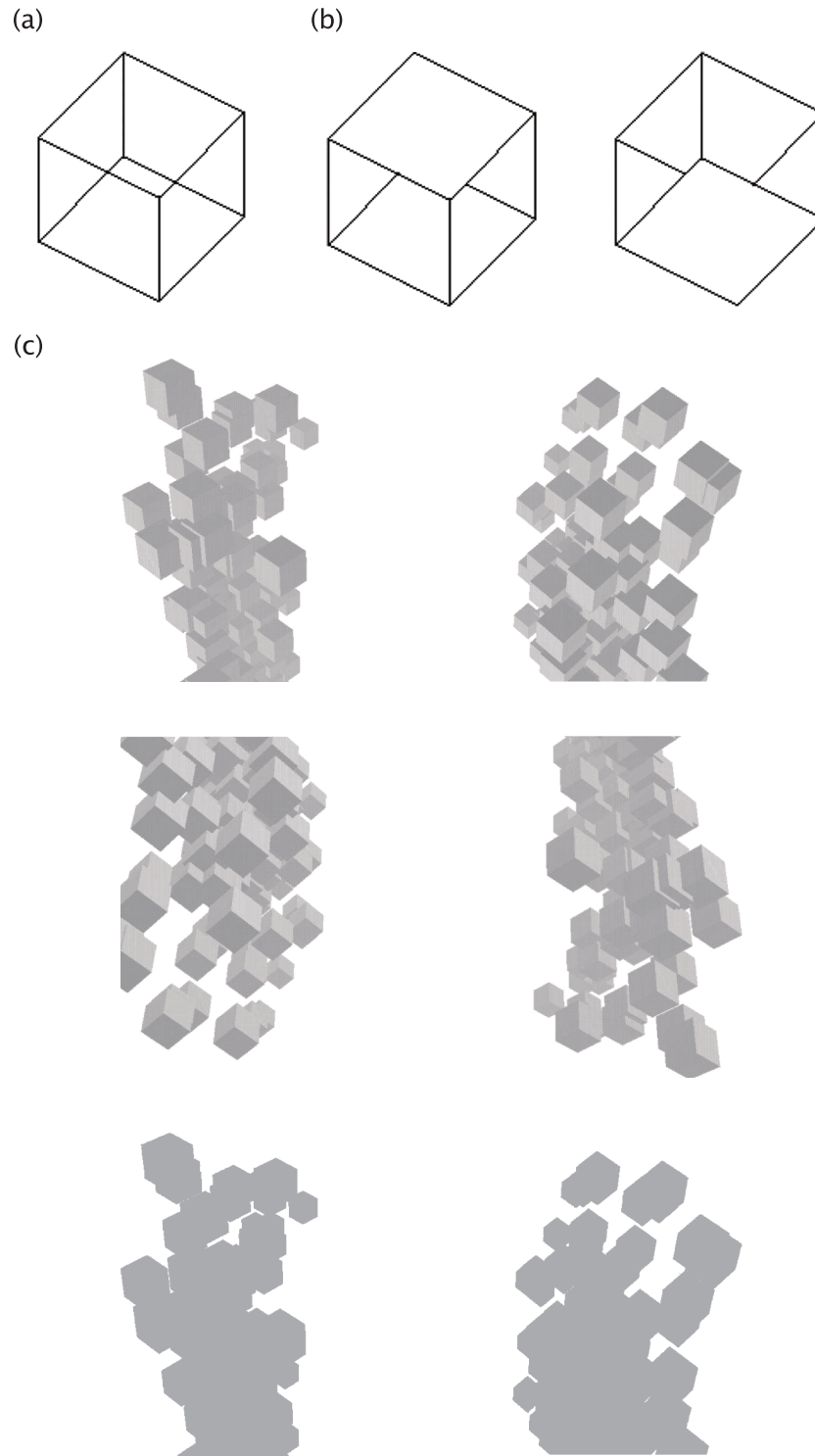


Fig. 4.1: Stimuli used in Experiment 1 and 2.

(a) The example of the main stimulus: A Necker cube stimulus was used that evoked bistable perception from above and below. (b) VFA (left) and VFB (right) cubes. In Experiment 1, they were presented before the stimulus (a) as a cue. They were created by removing some lines from (a) to aim to bias perception viewing from above or bottom. These stimuli were the same as flipping upside down and stimuli properties were the same. (a) and (b) were drawn with white edges in the experiment. (c) Examples of background contexts used in Experiment 2. One of the three background contexts (VFA: top, VFB, middle, Control; bottom) was presented around the stimulus of (a) randomly. The VFA and VFB stimuli are the same when reversed upside down. The control stimulus was filled to have the same luminance as the average luminance of other background stimuli.

Procedure

First, participants wore an HMD and adjusted the head belt according to the size of their heads. Thereafter, a five-point calibration was performed for acquiring the positions of both eyes and the eye gaze. The interpupillary distance was set to 64.1 mm, which is the average interpupillary distance for Japanese men [133]. Participants were seated in a chair and given a VIVE controller to hold. The experiment was performed in a 3D virtual space, but the stimuli were presented as a planar image. The fixation cross was shown for 1,000 ms, and then a cube with either the top or bottom side rendered opaque was presented for 1,000 ms as a cue (hereafter called “cue”). Two kinds of images were randomly used as cues: one yielded the perspective of a cube seen from above and the other a perspective from below. After the cue, the standard Necker cube was shown (by removing the surface shading while leaving the standard wireframe) for 2,000 ms. At its offset, participants reported, by pressing one of two forced-choice keys, which percept they saw initially and whether a reversal to the alternative perspective occurred while viewing the empty cube. The experiment consisted of two blocks: vertical and horizontal conditions according to the stimulus presentation positions. The stimuli’ presentation angle was set to 0 degrees with the head horizontal to the ground, and angle conditions were set to -60, -30, 0, 30, and 60 degrees (vertical and horizontal) in each block. The conditions were 20 (each cue type \times five angle types \times vertical and horizontal block), with 16 trials each for a total of 320 trials. Trials in the block were randomized, divided into four sessions, and sufficient breaks were given between sessions. The order between two blocks was counterbalanced by inverting it for every other participant. Participants were instructed to look at the center of the stimuli as much as possible during each trial. The timeline of one trial in Experiment 1 is shown in Figure 4.2a.

In Experiment 2, the background context and the Necker cube stimulus were used to investigate the relationship between the background context and posture. A fixation point was presented for 2,000 ms, a Necker cube with one of the three contexts for 3,000 ms, and then participants responded to the appearance of the Necker cube. The timeline of one trial in Experiment 2 is shown in Figure 4.2b.

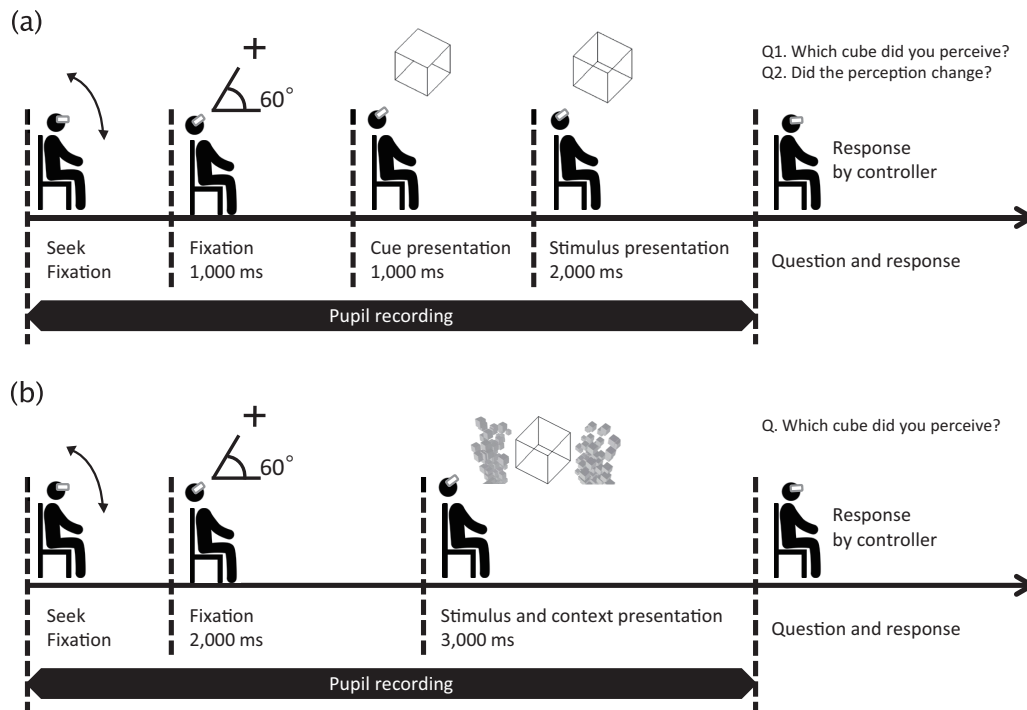


Fig. 4.2: Illustration of the timeline of the experiments.

(a) Flow of one trial in Experiment 1. Participants shook their heads and looked for a fixed fixation point at one of the five angles. In the example of the figure, it is a trial at 60 degrees. After 1,000 ms of gazing at the fixation point, a cue was presented for 1,000 ms, and then the stimulus was presented for 2,000 ms. Participants then responded about their perception. (b) The flow of one trial in Experiment 2. The general flow was similar to 1, but the fixation point was for two seconds, and the stimulus and background context were presented for three seconds concurrently. The question has been simplified to one.

4.2.2 Recording and Analysis

Behavioral Analysis

From the participants' key-press responses, I calculated the probability that they perceived the VFA appearance of the cube. A three-way repeated-measures ANOVA was conducted using the average probabilities for each cue (VFA and VFB), each angle (-60, -30, 0, 30, 60), and each direction (vertical and horizontal) as within-subject factors in Experiment 1. A two-way repeated-measures ANOVA was conducted using the average probabilities for each angle (-60, -30, 0, 30, 60) and each context (VFA, VFB, Control) as within-subject factors in Experiment

2. Pairwise comparisons for main effects were corrected for multiple comparisons using Shaffer's MSRB (Modified Sequentially Rejective Bonferroni) Method, and the level of statistical significance was set to $p < 0.05$ for all analyses. The Greenhouse-Geisser corrections were performed when the results of Mauchly's sphericity test were significant. The data were analyzed using Matlab 2018b (MathWorks, Natick, MA, USA) and R (4.0.2) with a tool for ANOVA (anovakun version 4.8.5).

Pupil recording and analysis

Pupil sizes and eye movements were measured during the task with Optional Corrective Lenses (VIVE Pro Eye with Tobii Eye Tracking, Tobii, Sweden) at a sampling rate of 120 Hz. Eye movements were monitored from both eyes. For analyses, I used pupil diameters from the left eyes. Interpolation was performed in the part where pupil diameter data could not be obtained due to eye blinking using cubic spline interpolation. Pupil recordings were smoothed using a sliding average (83.3 ms time window). Trials with a change in pupil diameter of more than 0.06 [mm/ms] were assumed to be artifacts and were excluded from the analysis. One participant's data, which had no trial in any of the conditions due to this analysis, was rejected from the analysis in Experiment 1. In the time-course analysis, each trial was normalized by subtracting pupil size at stimulus onset from the baseline pupil size. Baseline pupil size was computed as an average of data collected 200 ms prior to the stimulus onset (0 ms). This onset refers to the cue presentation in Experiment 1 and the stimulus presentation in Experiment 2. I calculated the time course of the trial's average pupils in all conditions (two cues, five angles, and two directions in Experiment 1). Specifically, the average pupil diameters from 1,000 ms to 3,000 ms after the cue presentation were calculated (during the stimulus presentation for two seconds), and a three-way repeated-measures ANOVA was performed to assess the presence of significant differences in pupil diameter with cue (VFA, VFB), angle (-60, -30, 0, 30, 60) and direction (vertical and horizontal) as within-subject factors in Experiment 1. Similarly, in Experiment 2, the averaged pupil diameter was calculated, and a two-way repeated-measures ANOVA was performed to assess the presence of significant differences in pupil diameter, with angle (-60, -30, 0, 30, and 60) and context (VFA, VFB, and Control). Pairwise comparisons for main effects in the ANOVA were corrected for multiple comparisons using Shaffer's MSRB method and the level of statistical significance was set to $p < 0.05$ for all analyses.

4.2.3 Results

Experiment 1

We first analyzed the average probability of VFA perception in each condition (Figure 4.3). A three-way ANOVA revealed a significant first-order interaction of averaged probability of VFA perception between direction and angle ($F_{(3.29,72.39)} = 4.29$, $p = 0.006$, $\eta_p^2 = 0.16$). Subsequent analysis showed that there was a simple main effect for angle in the vertical condition ($F_{(2.55,56.04)} = 6.29$, $p = 0.002$, $\eta_p^2 = 0.22$). Importantly, following a multiple comparison for angle in the vertical condition, the probability of VFA perception in the -30 and -60 degrees conditions were greater than in the 60 degrees condition ($t(22) = 3.33$, $p = 0.003$, $p_{adj} = 0.03$; $t(22) = 3.11$, $p = 0.005$, $p_{adj} = 0.03$, respectively). The ANOVA also revealed a significant main effect of the cue and angle condition (Cue: $F_{(1,22)} = 10.76$, $p = 0.003$, $\eta_p^2 = 0.32$; Angle: $F_{((1,22))} = 5.40$, $p = 0.003$, $\eta_p^2 = 0.20$). All other conditions and their interactions were nonsignificant.

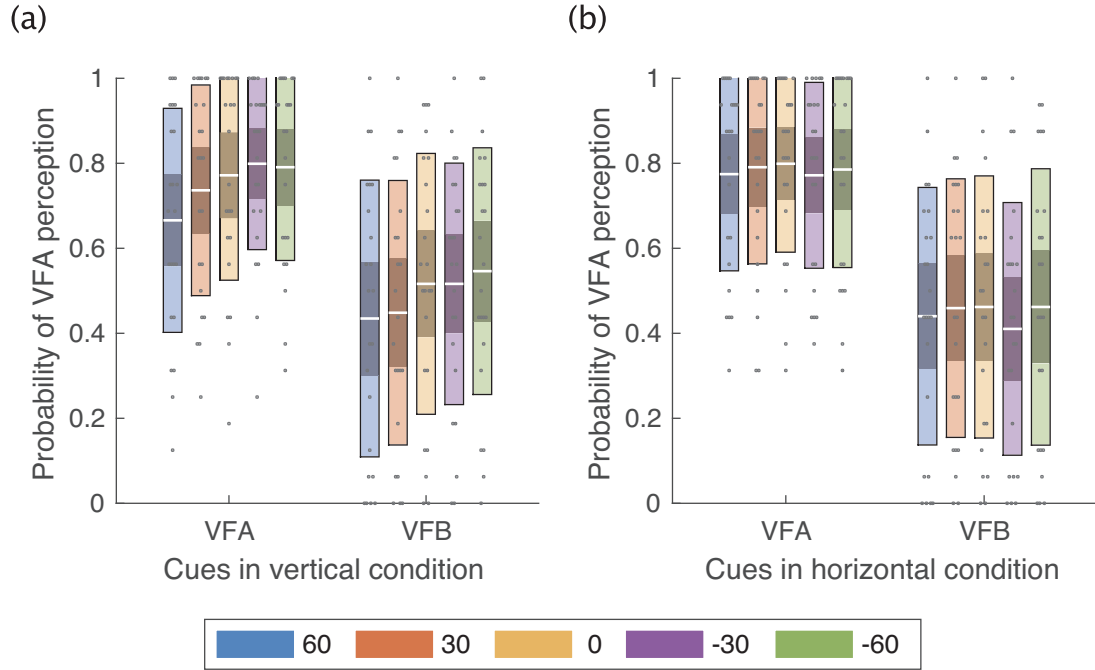


Fig. 4.3: Behavioral results in Experiment 1.

(a) The averaged probability of VFA perception between cue and angle conditions in the vertical condition across all participants. (b) The averaged probability of VFA perception between cue and angle conditions in the horizontal condition across all participants. The white line indicates the mean of participants, the light color indicates 1.96 SEM (95% confidence interval), and the dark color indicates 1 SD. Each grey dot indicates the mean of each participant. Each color represents the angle at which the stimulus was presented.

I then analyzed and compared the pupil diameter between the conditions (Figure 4.4). The three-way ANOVA revealed a significant first-order interaction of average pupil diameter between direction and angle ($F_{(2.40,50.36)} = 20.26, p < 0.0001, \eta_p^2 = 0.49$). Subsequent analysis showed that there was a simple main effect for angle in the vertical condition ($F_{(2.39,50.21)} = 27.24, p < 0.0001, \eta_p^2 = 0.56$). Importantly, following a multiple comparison for angle in the vertical condition, pupil diameter of -60 degrees was smaller than in all other conditions (vs. 60: $t(21) = 6.31, p < 0.0001, p_{adj} < 0.0001$; vs. 30: $t(21) = 6.95, p < 0.0001, p_{adj} < 0.0001$; vs. 0: $t(21) = 5.89, p < 0.0001, p_{adj} < 0.0001$; vs. -30: $t(21) = 5.05, p = 0.0001, p_{adj} = 0.0003$) (Figure 4.4c). Moreover, following a multiple comparison for angle in the vertical condition, pupil diameter in the -30 degrees condition was smaller than in the 60, 30 and 0 degrees conditions ($t(21) = 4.45, p = 0.0002, p_{adj} = 0.0009$; $t(21) = 5.23, p < 0.0001, p_{adj} = 0.0002$; $t(21) = 3.74, p = 0.0012, p_{adj} = 0.0049$, respectively). The multiple comparison also showed pupil diameter in the 0 degrees condition were smaller than in the 60 and 30 conditions ($t(21) = 2.77, p = 0.0114, p_{adj} = 0.0342$; $t(21) = 2.60, p = 0.0167, p_{adj} = 0.0342$, respectively). On the other hand, a simple main effect for the direction and angle interaction was not significant in the angle in the horizontal condition ($F_{(2.90,60.96)} = 0.78, p = 0.504, \eta_p^2 = 0.03$). Since there were many factors and the results were complicated, only the important results were shown here. See also Table 4.1, 4.2, 4.3, 4.4 for all statistics.

Taken together, our results suggested that the perception of Necker cubes changed depending on neck posture; however, there were two concerns. The first was the dynamics in the pupil diameter of early latency at the time of cueing, which may have reflected the noise of the movement of the neck before the stimulus presentation. The second concern was that the pupillary responses might include the effect of the cueing stimulus itself. To address this problem, in Experiment 2, we tried to reduce the noise of the movement by setting the head fixing time to be extended by two seconds. In addition, we tested whether the same effect can be obtained by changing the background context, instead of cueing, to confirm it was not a cue-specific effect.

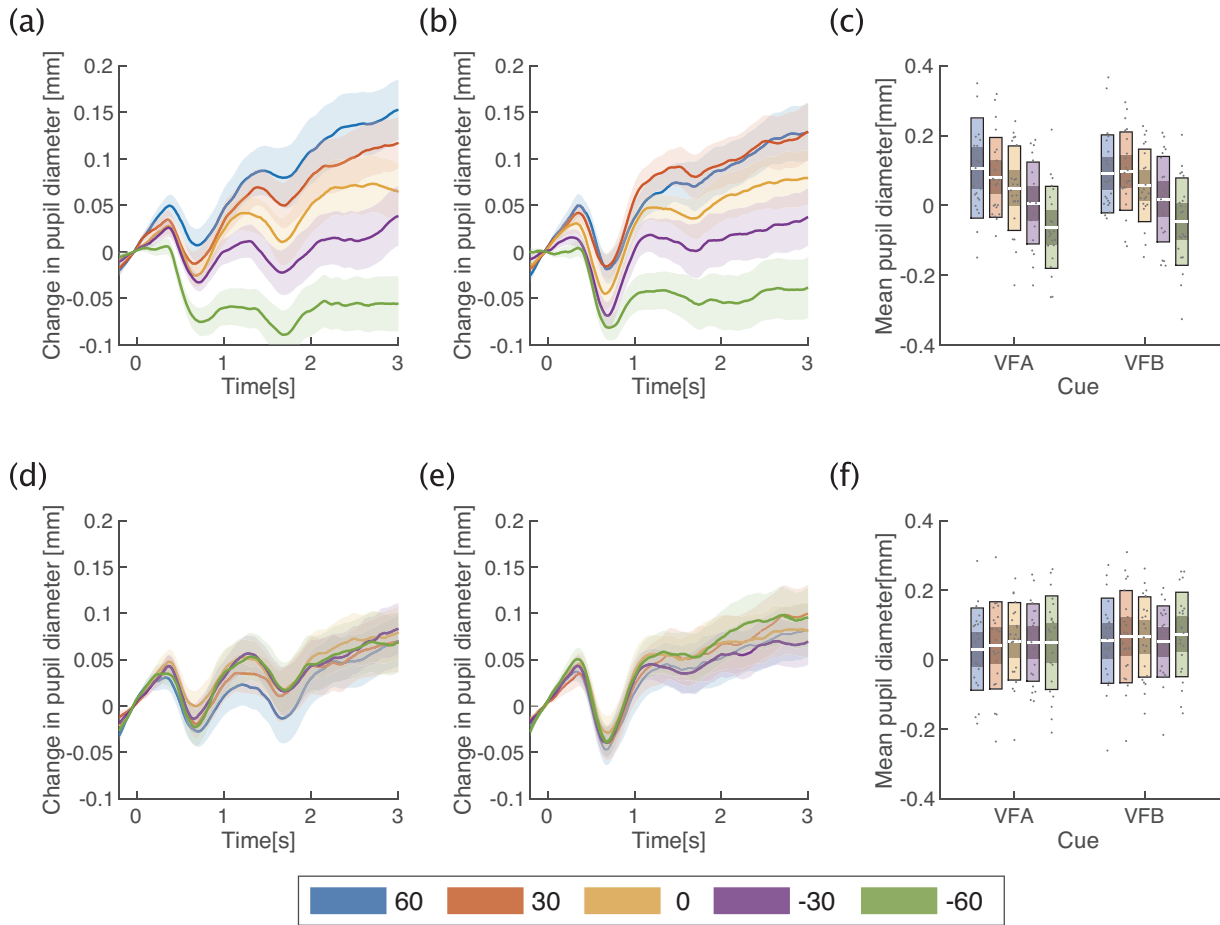


Fig. 4.4: Pupillary results in Experiment 1.

(a) Time course of averaged pupil diameter when cued VFA in the vertical condition across all participants. (b) Time course of averaged pupil diameter when cued VFB in the vertical condition across all participants. (c) Averaged pupil diameter from one to three seconds for each condition in the vertical condition. (d) Time course of averaged pupil diameter when cued VFA in the horizontal condition across all participants. (e) Time course of averaged pupil diameter when cued VFB in the horizontal condition across all participants. (f) Averaged pupil diameter from one second to three seconds for each condition in the horizontal condition. In (a), (b), (d), and (e), the line shows the average pupil diameter and the shaded color shows the standard error of the mean. In these figures, the cues were presented in the range from zero to one second, and the ambiguous Necker cube was presented from one to three seconds (the range of baseline was -200 ms to zero seconds, which was presented as the fixation point). In (c) and (f), the white line indicates the mean of participants, the light color indicates 1.96 SEM (95% confidence interval), the dark color indicates 1 SD, and each grey dot indicates the mean of each participant. Each color represents the angle at which the stimulus was presented.

Table 4.1: All ANOVA results from the pupillary analysis of Experiment 1.

Source	SS	df	ms	F value	p value	sig. ^l	p.eta^2
s	4.24	21.00	0.20	-	-	-	-
Direction	0.02	1.00	0.02	0.80	0.3819	ns	0.0366
s x Direction	0.56	21.00	0.03	-	-	-	-
Cue	0.02	1.00	0.02	4.84	0.0391	*	0.1874
s x Cue	0.07	21.00	0.00	-	-	-	-
Angle	0.30	2.81	0.11	17.21	0.0000	***	0.4504
s x Angle	0.37	59.11	0.01	-	-	-	-
Direction x Cue	0.00	1.00	0.00	3.38	0.0802	+	0.1386
s x Direction x Cue	0.02	21.00	0.00	-	-	-	-
Direction x Angle	0.40	2.40	0.17	20.26	0.0000	***	0.4910
s x Direction x Angle	0.42	50.36	0.01	-	-	-	-
Cue x Angle	0.01	3.23	0.00	0.72	0.5516	ns	0.0333
s x Cue x Angle	0.16	67.78	0.00	-	-	-	-
Direction x Cue x Angle	0.01	3.09	0.00	0.89	0.4511	ns	0.0409
s x Direction x Cue x Angle	0.17	64.87	0.00	-	-	-	-
Total	6.77	439.00	0.02	-	-	-	-

^l +p < .10, *p < .05, **p < .01, ***p < .001

Table 4.2: Simple effects for direction \times angle interaction from the pupillary analysis of Experiment 1.

Source	SS	df	ms	F value	p value	sig. ^l	p.eta^2
Direction at 60	0.07	1.00	0.07	6.09	0.0222	*	0.2249
s x Direction at 60	0.24	21.00	0.01	-	-		-
Direction at 30	0.03	1.00	0.03	1.76	0.1985	ns	0.0775
s x Direction at 30	0.33	21.00	0.02	-	-		-
Direction at 0	0.00	1.00	0.00	0.13	0.7216	ns	0.0062
s x Direction at 0	0.13	21.00	0.01	-	-		-
Direction at -30	0.03	1.00	0.03	8.47	0.0084	**	0.2874
s x Direction at -30	0.08	21.00	0.00	-	-		-
Direction at -60	0.29	1.00	0.29	30.74	0.0000	***	0.5942
s x Direction at -60	0.20	21.00	0.01	-	-		-
Angle at vertical	0.69	2.39	0.29	27.24	0.0000	***	0.5646
s x Angle at vertical	0.54	50.21	0.01	-	-		-
Angle at horizontal	0.01	2.90	0.00	0.78	0.5038	ns	0.0360
s x Angle at horizontal	0.25	60.96	0.00	-	-		-

^l +p < .10, *p < .05, **p < .01, ***p < .001

Table 4.3: Multiple comparisons for angle in the vertical condition from the pupillary analysis of Experiment 1.

pair	difference	t	df	p.value	adj.p	significance ^I
30--60	0.1439	6.95	21	0.0000	0.0000	30 > -60 *
60--60	0.1534	6.31	21	0.0000	0.0000	60 > -60 *
0--60	0.1080	5.89	21	0.0000	0.0000	0 > -60 *
30--30	0.0769	5.28	21	0.0000	0.0002	30 > -30 *
-30--60	0.0670	5.05	21	0.0001	0.0003	-30 > -60 *
60--30	0.0864	4.45	21	0.0002	0.0009	60 > -30 *
0--30	0.0410	3.74	21	0.0012	0.0049	0 > -30 *
60-0	0.0454	2.77	21	0.0114	0.0342	60 > 0 *
30-0	0.0359	2.60	21	0.0167	0.0342	30 > 0 *
60-30	0.0095	0.67	21	0.5078	0.5078	60 = 30

^I +p < .10, *p < .05, **p < .01, ***p < .001

Table 4.4: Multiple comparisons for the angle condition from the pupillary analysis of Experiment 1.

pair	difference	t	df	p.value	adj.p	significance ^I
30--60	0.0685	5.88	21	0.0000	0.0001	30 > -60 *
60--60	0.0676	5.23	21	0.0000	0.0002	60 > -60 *
30--30	0.0399	5.16	21	0.0000	0.0002	30 > -30 *
0--30	0.0247	4.58	21	0.0002	0.0010	0 > -30 *
0--60	0.0532	4.36	21	0.0003	0.0017	0 > -60 *
60--30	0.0391	3.87	21	0.0009	0.0036	60 > -30 *
-30--60	0.0285	2.49	21	0.0213	0.0850	-30 = -60
30-0	0.0153	1.86	21	0.0764	0.2293	30 = 0
60-0	0.0144	1.57	21	0.1324	0.2647	60 = 0
60-30	-0.0009	0.11	21	0.9161	0.9161	60 = 30

^I +p < .10, *p < .05, **p < .01, ***p < .001

Experiment 2

Similar to Experiment 1's analysis, I calculated and analysed the average probability of VFA perception in each condition (Figure 5). A two-way ANOVA showed a significant main effect of the probability in the context and angle conditions (Context: $F_{(1.41,25.35)} = 13.93$, $p = 0.0003$, $\eta_p^2 = 0.44$; Angle: $F_{(1.44,25.98)} = 13.77$, $p = 0.0003$, $\eta_p^2 = 0.43$). A multiple comparison for the context condition showed that the probability in the VFB condition was significantly smaller than in the VFA and control conditions (VFB vs VFA: $t(18) = 4.02$, $p = 0.0008$, $p_{adj} = 0.0024$; VFB vs Control: $t(18) = 3.91$, $p = 0.0010$, $p_{adj} = 0.0024$). In addition, a multiple comparison for the angle condition showed that the probability in the -60 and -30 degrees conditions were greater than in the 0, 30, and 60 degrees conditions (-60 vs 0: $t(18) = 4.73$, $p = 0.0002$, $p_{adj} = 0.0017$; -60 vs 30: $t(18) = 4.53$, $p = 0.0003$, $p_{adj} = 0.0017$; 60 vs -60: $t(18) = 4.43$, $p = 0.0003$, $p_{adj} = 0.0019$; -30 vs 0: $t(18) = 4.73$, $p = 0.0002$, $p_{adj} = 0.0017$; -30 vs 30: $t(18) = 4.12$, $p = 0.0006$, $p_{adj} = 0.0039$; -30 vs 60: $t(18) = 3.99$, $p = 0.0009$, $p_{adj} = 0.0039$). All other conditions and their interactions were nonsignificant.

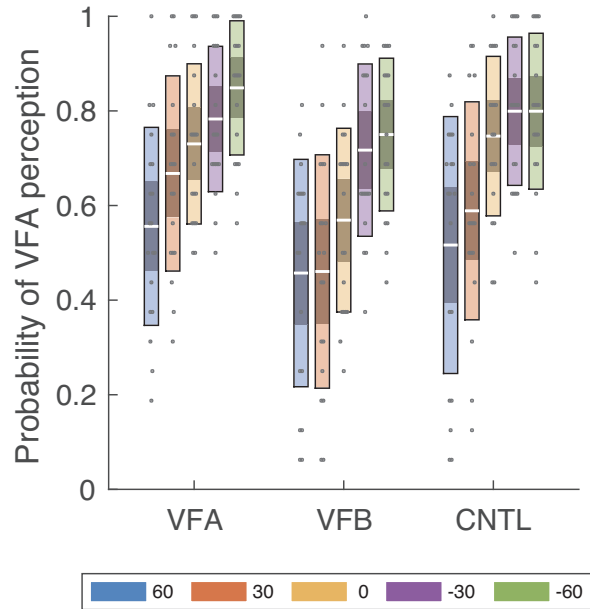


Fig. 4.5: The averaged probability of VFA perception between the cue and angle conditions across all participants in Experiment 2.

The white line indicates the mean of participants, the light color indicates 1.96 SEM (95% confidence interval), and the dark color indicates 1 SD. Each grey dot indicates the mean of each participant. Each color represents the angle at which the stimulus was presented.

The pupillary data were also analysed for each condition as in Experiment 1 (Figure 6). A two-way ANOVA showed a significant main effect of average pupil diameter both in the context and angle conditions (Context: $F_{(1.69,30.49)} = 6.10$, $p = 0.0083$, $\eta_p^2 = 0.25$; Angle: $F_{(2.32,41.73)} = 8.11$, $p = 0.0006$, $\eta_p^2 = 0.31$). Interestingly, a multiple comparison for the context condition showed that the average pupil diameter in the control condition was significantly greater than the VFA and VFB conditions, unlike the behavioral results (Control vs VFA $t(18) = 2.55$, $p = 0.0197$, $p_{adj} = 0.0197$; Control vs VFB $t(18) = 3.71$, $p = 0.0016$, $p_{adj} = 0.0048$). Additionally, a multiple comparison for the angle condition showed that the average pupil diameter in the -60 degrees condition was significantly smaller than all other angle conditions (-60 vs 60 $t(18) = 3.32$, $p = 0.0038$, $p_{adj} = 0.0230$; -60 vs 30: $t(18) = 3.62$, $p = 0.0020$, $p_{adj} = 0.0118$; -60 vs 0: $t(18) = 5.67$, $p < 0.0001$, $p_{adj} = 0.0002$; -60 vs -30: $t(18) = 4.82$, $p = 0.0001$, $p_{adj} = 0.0008$). All other conditions and their interactions were nonsignificant.

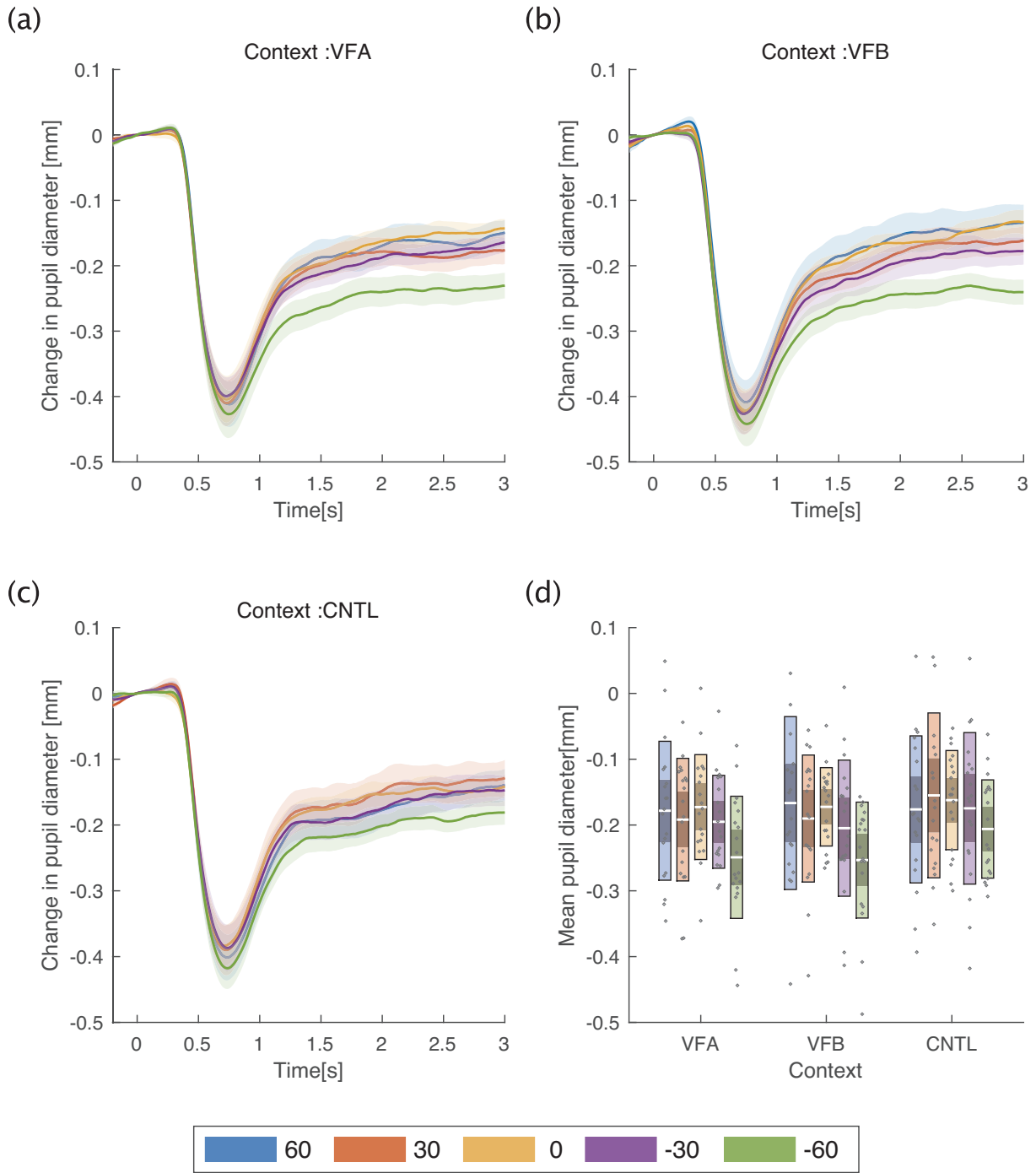


Fig. 4.6: Pupillary results in Experiment 2.

(a) Time course of averaged pupil diameter when VFA context across all participants. (b) Time course of averaged pupil diameter when VFB context across all participants. (c) Time course of averaged pupil diameter when Control context across all participants. (d) Averaged pupil diameter from one to three seconds for each condition in the vertical condition. In (a) and (b), the line shows the average pupil diameter, and the shaded color shows the standard error of the mean. In (c), the white line indicates the mean of participants, the light color indicates 1.96 SEM (95% confidence interval), the dark color indicates 1 SD, and each grey dot indicates the mean of each participant. Each color represents the angle at which the stimulus was presented.

4.2.4 Discussion

Neck posture modulates the effects of perceptual bias

The purpose of this study was to clarify the relationship between neck posture and visual heuristics and investigated the perception of the appearance of Necker cubes placed in VR space in various neck postures. As a result of Experiment 1, when looking down (at -60 and -30 degrees), the probability of VFA perception of the Necker cube was significantly greater than when looking up (at 60 degrees). Furthermore, the same effect was replicated in Experiment 2 (The VFA probability in the -60 and -30 degrees conditions were greater than 0, 30, and 60 degrees in the angle condition). Simply put, our experiments demonstrated that the effects of perceptual bias differ depending on neck posture, even though the stimuli presented on the retinal information was the same.

In a previous paper that investigated the perception of the inverted state of the head (by viewing from between the legs), the difference in perception from the normal posture was explained by the change in the proprioceptive sensation of the head for an abnormal state [125, 126]. The physiological basis of this hypothesis is that proprioceptive information from the somatosensory area in the postcentral gyrus is integrated with visual information (e.g., Dijkerman de Haan, 2007 [134]; Zangaladze, Epstein, Grafton, Sathian, 1999 [135]). In our experiments, the normal neck angle used in daily life was adopted, but the effect of perceptual bias was changed. Thus, the proprioceptive sensation of the head is more sensitive than previously considered and may be adopted, even in normal postures, to shape perception.

In addition, one of the rational interpretations of our results is the Bayesian theory of perception [112]. In previous studies, the perceptual probabilities of the appearance of ambiguous figures were explained by this theory [64]. In the present study, the interpretation of the Necker cube was explained by interpretation parameters combined, prior and posterior distribution, over time as a perceptual decision-making model. Moreover, it is known that an observer's prior information and environmental distribution corresponded [114]. These results indicate that it can also be explained by extending the Bayesian theory of perception. That is, I consider that neck posture is incorporated in the Bayesian theory of perception as a variable that influences perceptual stability. To illustrate, in daily life, we look down to see the appearance of the VFA

cube. Conversely, the VFB cube can also be seen by looking up. Thus, it can be interpreted that such perceptual experience and posture are linked and affect long-term memory related to our perception.

The size of the pupil diameter is also consistent with perception probability

Interestingly, the pupil diameter was significantly smaller in the looking down condition (in the case of the -60 degrees condition compared with other pupil diameters and in the case of the -30 degrees condition compared with the 0, 30, and 60 degrees conditions). Contrary to what I expected, the large change of pupil diameter in Experiment 1 was evoked before the stimulus presentation. This early pupillary response is assumed to be due to neck movement rather than visual stimulation considering the latency of the pupil diameter. In fact, in Experiment 2, as the head fixation before the presentation of the stimulus was extended to two seconds, the baseline of the pupil diameter aligned. This difference in this early pupil diameter might reflect the locus coeruleus (LC)-norepinephrine (NE) system which evokes an inhibitory effect on the parasympathetic oculomotor complex by the release of norepinephrine from the LC, which is also involved in postural control [107,136,137]. The LC is also involved in postural control [138]. In addition, noradrenergic LC neurons are also involved in the vestibulo-autonomic reflex [139]. Thus, our results indicated that the modulation of the LC activity caused by the postural control of the neck changed pupil diameter.

It is important to further consider whether this pupillary change is directly related to perceptual change. The pupils are the window of visual inputs, and in previous studies, pupil diameter had a direct effect on the feedforward response in the early visual cortex independent of psychological factors [140]. This poses the following questions: is it directly related to the fact that the size of the pupil is consistent with perception? Or is it the outcome of cognitively reflecting the subject's perception? These points should be further investigated in future studies.

In the result of Experiment 2, except for the early change in pupil diameter that was expected to be caused by postural control, the average pupil diameter in the control condition was significantly greater than in both the VFA and VFB conditions. Since the brightness of these background contexts was controlled to be the same, it can be deduced that there is almost

no physical intensity of light effect on the pupil diameter. Background contexts are known to contribute to perceptual stability [64, 141]; therefore, the attentional load is considered to be greater with no context than with a context. In addition, increased attentional effort dilates pupil diameter [83, 111, 142]. Therefore, our results could be interpreted as the attentional load reflected in the pupil diameter.

This study had several limitations that should be considered. Firstly, the change in pupil diameter was unexpected before the stimulus was presented. In Experiment 2, considering that the baseline was almost the same after two seconds of moving the neck, the change subsided within two seconds after the change in neck posture. However, the exact latency and amount of change in pupil diameter due to the change of the neck remains unclear. Thus, further research is needed to investigate the details of this change in pupil diameter. Secondly, the vertical movement of the neck caused a difference in perception; however, it was unclear whether this was due to the direction of gravity, related to the position of the stimuli: the top and bottom, or due to the body coordinate system. Consequently, further research is needed on whether not only the posture of the neck but also the posture of the whole body affects perceptual bias.

4.2.5 Conclusion

The purpose of this study was to clarify the relationship between neck posture and visual heuristics from the aspects of both behavioral response and pupil diameter, an established physiological cognitive index. Our results showed that the probability of the viewing-from-above bias perception of the Necker cube was significantly greater when looking down than when looking up. Interestingly, the pupillary results were also consistent with the probability of perception. These results indicate that perception was modulated by neck posture and suggest that neck posture is incorporated into ecological constraints. To our knowledge, this is the first study to link pupil diameter, perceptual heuristics, and posture. This indicates that postural changes affect perception and that pupil changes intervene to track the perceptual changes. Besides, by investigating cognitive processing in various postures and movements in VR space, the relationship between body and perception will become clearer.

Chapter 5

Conclusion

In this thesis, we aimed to quantify subjective perception through the experiments in Chapters 2, 3, and 4. Since it is difficult to directly measure the perceptual contents, in this study, an index of attentional state such as EEG and pupil diameter was used to estimate the perceptual contents.

Specifically, I investigated the simultaneous measurement of EEG and pupil diameter in ambiguous figures. Additionally, I investigated the perceptual bias when observing ambiguous figures using pupillometry. Furthermore, this study was extended to conditions with changes in neck posture using a VR environment. In this section, I summarize the findings and contribution of my study. In addition, I describe how my findings help quantify subjective perception.

5.1 Summary

Perceptual Switches predicted using the SSVEP and Pupillometry

In order to clarify the relationship between attentional state and the pupil diameter during participant observed bistable figure, in this study, I performed the measurement of SSVEP and the pupil diameter simultaneously. Rotating sphere stimuli (RDK stimulus) composed of flickering dots with black and white for tracking pupillary change was used as the presentation stimulus. Resultantly, a significant difference was found in the SSVEP amplitude during left-right rotated perception. Furthermore, a change in pupil diameter seems to be a shift of attention target before observer response of perceptual switches. These results indicated that shift of attention might be the trigger for the perceptual switches.

Pupil measurement on the cueing Necker cubes

I hypothesized that a perceptually ambiguous or bistable object (Necker cube) can be more effectively biased in assuming a point of view-from-above (VFA) than from below the object, by cueing attention. In the results of my experiment, I found the presence of a VFA bias with forced attention, which was accompanied by reduced attentional effort, as indexed by a reduced pupil diameter, compared with the view-from-below. On the other hand, participants showed no bias during passive viewing. From these pieces of evidence, I suggested that the level of intensive attention, when retrieving and maintaining a specific view from memory, is mirrored in the size of the eye pupils and may reflect ecological constraints on visual perception.

The bias of ambiguous figure and posture

In this study, I investigated how perceptual bias and experiential contexts of human perception affect the observer's perception when the posture is changed. I hypothesized that a change in the perceptual probability caused by perceptual bias also depends on posture. To verify this hypothesis, I focused on the Necker cube, which can be interpreted as two types of appearance from above and below although the input is constant, and investigated the change of the probability of perceptual content. Specifically, I conducted it by asking observers their perception of the appearance of the Necker cube, placed at any of the five angles in the space of virtual reality with pupillometry. Consequently, during the condition of looking down vertically, the probability of viewing-from-above perception of the Necker cube was significantly greater than during the condition of looking up. Interestingly, the pupillary results were also consistent with the probability of the perception. These results indicate that perception is modulated by the posture of the neck and suggest that neck posture is incorporated into ecological constraints.

5.2 Towards the quantification of subjective perception

Here, I discuss how my study could have contributed to subjective quantification and what should be done in the future to quantify subjective perception.

The contribution of this study to the quantification of subjective perception can be summarized in the following two points. First, I showed that subjective perception could be extracted

by using SSVEP stimuli to extract attentional states. Second, I also found that perceptual bias related to subjective perception can be extracted from the pupillary response, one of the physiological indices. Specifically, I showed that perceptual bias could be extracted under specific attentional conditions. Furthermore, I found that the strength of the perceptual bias depends on changes in neck posture. It was essential that I was able to find conditions under which these physiological indices correlate with subjective perception.

However, some limitations should be noted. First, this study examined a method for extracting subjective perception, and the above points were clarified to conduct statistical analysis. It is desirable to make it possible to extract at the single-trial level in the future. As one approach to realize this, I believe that combining measure eye movements, such as optokinetic nystagmus (OKN), with this study may provide richer information and enable estimation of subjective perception with higher accuracy. For example, recent study showed transparent motion could be estimated by pupil diameter and eye movements [58]. Interestingly, it mentions that the pupil response and OKN have different latency. This difference in response means that each has distinct characteristics, which may be helpful for perceptual estimation.

Second, there were individual differences in the performance of participants' tasks. Therefore, it is necessary to consider an experimental paradigm and analysis to focus on individual differences. Further investigation would lead to identifying factors for resolving the ambiguity and why individual differences occur. These also will help quantify the subjective perception.

Third, I aimed to extract the perceptual content itself from the physiological index in this study. Still, as a result, I only extracted the attentional states correlated with the perceptual contents. In order to extract perceptual contents itself, it is important to understand how the mechanisms of subjective perception are produced. This is an issue to be resolved in future research.

Finally, in this study, I focused on ambiguous figures and estimated participants' perceptions. However, in reality, it is necessary to estimate richer information. Techniques for decoding and reconstructing what the observer sees are also important, rather than a selection task such as two-alternative forced choice. In recent years, with the development of deep learning, the appearance of humans has been reconstructed from fMRI brain images in the visual

cortex [143](however, it is necessary to discuss whether the information in the early visual cortex represents subjective perception). Such techniques may help reconstruct subjective perception in the future.

Bibliography

- [1] BR Conway, et al. Why do we care about the colour of the dress. *The Guardian*, 2015.
- [2] Rosa Lafer-Sousa, Katherine L Hermann, and Bevil R Conway. Striking individual differences in color perception uncovered by ‘the dress’ photograph. *Current Biology*, Vol. 25, No. 13, pp. R545–R546, 2015.
- [3] Frank Tong, Ming Meng, and Randolph Blake. Neural bases of binocular rivalry. *Trends in cognitive sciences*, Vol. 10, No. 11, pp. 502–511, 2006.
- [4] Louis Albert Necker. Lxi. observations on some remarkable optical phænomena seen in switzerland; and on an optical phænomenon which occurs on viewing a figure of a crystal or geometrical solid. *The London, Edinburgh, and Dublin Philosophical Magazine and Journal of Science*, Vol. 1, No. 5, pp. 329–337, 1832.
- [5] Edgar Rubin. Synsoplevede figurer. 1915.
- [6] Giambattista Della Porta. *De refractione optices parte libri novem*. Ex officina Horatii Salviani, apud Jo. Jacobum Carlinum, & Antonium Pacem, 1593.
- [7] Nicholas J Wade. Early studies of eye dominances. *Laterality: Asymmetries of body, brain and cognition*, Vol. 3, No. 2, pp. 97–108, 1998.
- [8] Charles Wheatstone. Contributions to the physiology of vision.—part the first. on some remarkable, and hitherto unobserved, phenomena of binocular vision. *Philosophical Transactions of the Royal Society of London*, Vol. 128, pp. 371–394, 1838.
- [9] Randolph Blake. A neural theory of binocular rivalry. *Psychological review*, Vol. 96, No. 1, p. 145, 1989.
- [10] H von Helmholtz. Concerning the perceptions in general. treatise on physiological optics. 1866.
- [11] Willem JM Levelt. *On binocular rivalry*. PhD thesis, Van Gorcum Assen, 1965.
- [12] William James, Frederick Burkhardt, Fredson Bowers, and Ignas K Skrupskelis. *The principles of psychology*, Vol. 1. Macmillan London, 1890.
- [13] Burtis Burr Breese. On inhibition. *Psychological Monographs: General and Applied*, Vol. 3,

- No. 1, 1899.
- [14] BB Breese. Binocular rivalry. *Psychological Review*, Vol. 16, No. 6, p. 410, 1909.
 - [15] Randolph Blake and Hugh Wilson. Binocular vision. *Vision research*, Vol. 51, No. 7, pp. 754–770, 2011.
 - [16] Ilona Kovács, Thomas V Papathomas, Ming Yang, and Ákos Fehér. When the brain changes its mind: Interocular grouping during binocular rivalry. *Proceedings of the National Academy of Sciences*, Vol. 93, No. 26, pp. 15508–15511, 1996.
 - [17] Nikos K Logothetis, David A Leopold, and David L Sheinberg. What is rivalling during binocular rivalry? *Nature*, Vol. 380, No. 6575, pp. 621–624, 1996.
 - [18] Randolph Blake and Nikos K Logothetis. Visual competition. *Nature Reviews Neuroscience*, Vol. 3, No. 1, pp. 13–21, 2002.
 - [19] Teng Leng Ooi and Zijiang J He. A distributed intercortical processing of binocular rivalry: psychophysical evidence. *Perception*, Vol. 32, No. 2, pp. 155–166, 2003.
 - [20] Hugh R Wilson. Computational evidence for a rivalry hierarchy in vision. *Proceedings of the National Academy of Sciences*, Vol. 100, No. 24, pp. 14499–14503, 2003.
 - [21] Francis Crick and Christof Koch. Towards a neurobiological theory of consciousness. In *Seminars in the Neurosciences*, Vol. 2, pp. 263–275. Saunders Scientific Publications, 1990.
 - [22] Francis Crick and Christof Koch. Consciousness and neuroscience. *Cerebral cortex*, Vol. 8, No. 2, pp. 97–107, 1998.
 - [23] Johan Wagemans, James H Elder, Michael Kubovy, Stephen E Palmer, Mary A Peterson, Manish Singh, and Rüdiger von der Heydt. A century of gestalt psychology in visual perception: I. perceptual grouping and figure–ground organization. *Psychological bulletin*, Vol. 138, No. 6, p. 1172, 2012.
 - [24] E Rubin. Visuell wahrgenommene figuren [visually perceived figures]. *Copenhagen, Denmark: Gylldendal*, 1921.
 - [25] Nava Rubin. Figure and ground in the brain. *Nature neuroscience*, Vol. 4, No. 9, pp. 857–858, 2001.
 - [26] Johan Wagemans. Historical and conceptual background: Gestalt theory. *The Oxford handbook of perceptual organization*, pp. 3–20, 2015.
 - [27] JC Flügel. The influence of attention in illusions of reversible perspective. *British Journal of Psychology*, Vol. 5, No. 4, p. 357, 1913.
 - [28] Anna Vicholkovska. Illusions of reversible perspective. *Psychological Review*, Vol. 13,

- No. 4, p. 276, 1906.
- [29] Gerald M Long and Thomas C Toppino. Enduring interest in perceptual ambiguity: alternating views of reversible figures. *Psychological bulletin*, Vol. 130, No. 5, p. 748, 2004.
 - [30] Margaret Floy Washburn, H Mallay, and A Naylor. The influence of the size of an outline cube on the fluctuations of its perspective. *The American Journal of Psychology*, pp. 484–489, 1931.
 - [31] Thomas C Toppino and Gerald M Long. Top-down and bottom-up processes in the perception of reversible figures: Toward a hybrid model. In *Dynamic cognitive processes*, pp. 37–58. Springer, 2005.
 - [32] Jürgen Kornmeier and Michael Bach. The necker cube—an ambiguous figure disambiguated in early visual processing. *Vision research*, Vol. 45, No. 8, pp. 955–960, 2005.
 - [33] Erik D Lumer, Karl J Friston, and Geraint Rees. Neural correlates of perceptual rivalry in the human brain. *Science*, Vol. 280, No. 5371, pp. 1930–1934, 1998.
 - [34] Erik D Lumer and Geraint Rees. Covariation of activity in visual and prefrontal cortex associated with subjective visual perception. *Proceedings of the National Academy of Sciences*, Vol. 96, No. 4, pp. 1669–1673, 1999.
 - [35] Philipp Sterzer and Andreas Kleinschmidt. A neural basis for inference in perceptual ambiguity. *Proceedings of the National Academy of Sciences*, Vol. 104, No. 1, pp. 323–328, 2007.
 - [36] CM Portas, BA Strange, KJ Friston, Raymond J Dolan, and CD Frith. How does the brain sustain a visual percept? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, Vol. 267, No. 1446, pp. 845–850, 2000.
 - [37] Abhrajeev V Roy, Keith W Jamison, Sheng He, Stephen A Engel, and Bin He. Deactivation in the posterior mid-cingulate cortex reflects perceptual transitions during binocular rivalry: Evidence from simultaneous eeg-fmri. *NeuroImage*, Vol. 152, pp. 1–11, 2017.
 - [38] Megan Wang, Daniel Arteaga, and Biyu J He. Brain mechanisms for simple perception and bistable perception. *Proceedings of the National Academy of Sciences*, Vol. 110, No. 35, pp. E3350–E3359, 2013.
 - [39] Diego Cosmelli, Olivier David, Jean-Philippe Lachaux, Jacques Martinerie, Line Garnero, Bernard Renault, and Francisco Varela. Waves of consciousness: ongoing cortical patterns during binocular rivalry. *Neuroimage*, Vol. 23, No. 1, pp. 128–140, 2004.
 - [40] Takamitsu Watanabe. Causal roles of prefrontal cortex during spontaneous perceptual

- switching are determined by brain state dynamics. *Elife*, Vol. 10, p. e69079, 2021.
- [41] Jan Brascamp, Philipp Sterzer, Randolph Blake, and Tomas Knapen. Multistable perception and the role of the frontoparietal cortex in perceptual inference. *Annual review of psychology*, Vol. 69, pp. 77–103, 2018.
 - [42] Philipp Sterzer, Andreas Kleinschmidt, and Geraint Rees. The neural bases of multistable perception. *Trends in cognitive sciences*, Vol. 13, No. 7, pp. 310–318, 2009.
 - [43] Theofanis I Panagiotaropoulos, Gustavo Deco, Vishal Kapoor, and Nikos K Logothetis. Neuronal discharges and gamma oscillations explicitly reflect visual consciousness in the lateral prefrontal cortex. *Neuron*, Vol. 74, No. 5, pp. 924–935, 2012.
 - [44] Ned Block. What is wrong with the no-report paradigm and how to fix it. *Trends in Cognitive Sciences*, Vol. 23, No. 12, pp. 1003–1013, 2019.
 - [45] Theofanis I Panagiotaropoulos, Abhilash Dwarakanath, and Vishal Kapoor. Prefrontal cortex and consciousness: beware of the signals. *Trends in cognitive sciences*, Vol. 24, No. 5, pp. 343–344, 2020.
 - [46] Matthias Michel and Jorge Morales. Minority reports: Consciousness and the prefrontal cortex. *Mind & Language*, Vol. 35, No. 4, pp. 493–513, 2020.
 - [47] Tomas Knapen, Jan Brascamp, Joel Pearson, Raymond van Ee, and Randolph Blake. The role of frontal and parietal brain areas in bistable perception. *Journal of Neuroscience*, Vol. 31, No. 28, pp. 10293–10301, 2011.
 - [48] Stefan Frässle, Jens Sommer, Andreas Jansen, Marnix Naber, and Wolfgang Einhäuser. Binocular rivalry: frontal activity relates to introspection and action but not to perception. *Journal of Neuroscience*, Vol. 34, No. 5, pp. 1738–1747, 2014.
 - [49] Jan Brascamp, Randolph Blake, and Tomas Knapen. Negligible fronto-parietal bold activity accompanying unreportable switches in bistable perception. *Nature neuroscience*, Vol. 18, No. 11, pp. 1672–1678, 2015.
 - [50] Melanie Boly, Marcello Massimini, Naotsugu Tsuchiya, Bradley R Postle, Christof Koch, and Giulio Tononi. Are the neural correlates of consciousness in the front or in the back of the cerebral cortex? clinical and neuroimaging evidence. *Journal of Neuroscience*, Vol. 37, No. 40, pp. 9603–9613, 2017.
 - [51] Christof Koch, Marcello Massimini, Melanie Boly, and Giulio Tononi. Neural correlates of consciousness: progress and problems. *Nature Reviews Neuroscience*, Vol. 17, No. 5, pp. 307–321, 2016.

-
- [52] Peng Zhang, Keith Jamison, Stephen Engel, Bin He, and Sheng He. Binocular rivalry requires visual attention. *Neuron*, Vol. 71, No. 2, pp. 362–369, 2011.
 - [53] Jinyou Zou, Sheng He, and Peng Zhang. Binocular rivalry from invisible patterns. *Proceedings of the National Academy of Sciences*, Vol. 113, No. 30, pp. 8408–8413, 2016.
 - [54] Masataka Watanabe, Kang Cheng, Yusuke Murayama, Kenichi Ueno, Takeshi Asamizuya, Keiji Tanaka, and Nikos Logothetis. Attention but not awareness modulates the bold signal in the human v1 during binocular suppression. *Science*, Vol. 334, No. 6057, pp. 829–831, 2011.
 - [55] Christof Koch and Naotsugu Tsuchiya. Attention and consciousness: two distinct brain processes. *Trends in cognitive sciences*, Vol. 11, No. 1, pp. 16–22, 2007.
 - [56] Jeroen JA Van Boxtel. Different signal enhancement pathways of attention and consciousness underlie perception in humans. *Journal of neuroscience*, Vol. 37, No. 24, pp. 5912–5922, 2017.
 - [57] Marco Turi, David Charles Burr, and Paola Binda. Pupillometry reveals perceptual differences that are tightly linked to autistic traits in typical adults. *Elife*, Vol. 7, p. e32399, 2018.
 - [58] Kei Kanari and Hirohiko Kaneko. Pupil response is modulated with optokinetic nystagmus in transparent motion. *JOSA A*, Vol. 38, No. 2, pp. 149–156, 2021.
 - [59] Wolfgang Einhäuser, James Stout, Christof Koch, and Olivia Carter. Pupil dilation reflects perceptual selection and predicts subsequent stability in perceptual rivalry. *Proceedings of the National Academy of Sciences*, Vol. 105, No. 5, pp. 1704–1709, 2008.
 - [60] Ken Nakayama and Shinsuke Shimojo. Experiencing and perceiving visual surfaces. *Science*, Vol. 257, No. 5075, pp. 1357–1363, 1992.
 - [61] Vilayanur S Ramachandran. Perception of shape from shading. *Nature*, Vol. 331, No. 6152, p. 163, 1988.
 - [62] Nikolaus F Troje and Matthew McAdam. The viewing-from-above bias and the silhouette illusion. *i-Perception*, Vol. 1, No. 3, pp. 143–148, 2010.
 - [63] Jürgen Kornmeier, Christine Maira Hein, and Michael Bach. Multistable perception: when bottom-up and top - down coincide. *Brain and cognition*, Vol. 69, No. 1, pp. 138–147, 2009.
 - [64] Rashmi Sundareswara and Paul R Schrater. Perceptual multistability predicted by search model for bayesian decisions. *Journal of vision*, Vol. 8, No. 5, pp. 12–12, 2008.
 - [65] Lauri Parkkonen, Jesper Andersson, Matti Hämäläinen, and Riitta Hari. Early visual brain

- areas reflect the percept of an ambiguous scene. *Proceedings of the National Academy of Sciences*, Vol. 105, No. 51, pp. 20500–20504, 2008.
- [66] Paola Binda, Maria Pereverzeva, and Scott O Murray. Pupil size reflects the focus of feature-based attention. *Journal of neurophysiology*, Vol. 112, No. 12, pp. 3046–3052, 2014.
- [67] David A Leopold, Melanie Wilke, Alexander Maier, and Nikos K Logothetis. Stable perception of visually ambiguous patterns. *Nature neuroscience*, Vol. 5, No. 6, pp. 605–609, 2002.
- [68] Maartje C de Jong, Zoe Kourtzi, and Raymond van Ee. Perceptual experience modulates cortical circuits involved in visual awareness. *European Journal of Neuroscience*, Vol. 36, No. 12, pp. 3718–3731, 2012.
- [69] David H Brainard and Spatial Vision. The psychophysics toolbox. *Spatial vision*, Vol. 10, pp. 433–436, 1997.
- [70] A. Delorme and S. Makeig. an open source toolbox for analysis of single-trial eeg dynamics including independent component analysis. *Journal of Neurosci Methods*, Vol. 134, No. 1, pp. 9–21, 2004.
- [71] Hugh Nolan, Robert Whelan, and RB Reilly. Faster: fully automated statistical thresholding for eeg artifact rejection. *Journal of neuroscience methods*, Vol. 192, No. 1, pp. 152–162, 2010.
- [72] Oostenveld R., Fries P., Maris E., and Schoffelen J. M. Fieldtrip: Open source software for advanced analysis of meg, eeg, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, Vol. 2011, p. 1, 2011.
- [73] Brunskill E. Krug K., Scarna A., Goodwin G. M., and Parker A. J. Perceptual switch rates with ambiguous structure-from-motion figures in bipolar disorder. *Proceedings of the Royal Society of London B: Biological Sciences*, Vol. 275, No. 1645, pp. 1839–1848, 2008.
- [74] C. Gundlach and M. M. Müller. Perception of illusory contours forms intermodulation responses of steady state visual evoked potentials as a neural signature of spatial integration. *Biological Psychology*, Vol. 94, No. 1, pp. 55–60, 2013.
- [75] R Duncan Luce, et al. *Response times: Their role in inferring elementary mental organization*. No. 8. Oxford University Press on Demand, 1986.
- [76] Koji Kadota and Hiroaki Gomi. Implicit visuomotor processing for quick online reactions is robust against aging. *Journal of Neuroscience*, Vol. 30, No. 1, pp. 205–209, 2010.

-
- [77] E. D. Freeman, P. Sterzer, and J. Driver. fMRI correlates of subjective reversals in ambiguous structure-from-motion. *Journal of Vision*, Vol. 12, No. 6, pp. 1–19, 2012.
 - [78] Nobuo Kawabata, Kiyoshi Yamagami, and Morikazu Noaki. Visual fixation points and depth perception. *Vision Research*, 1978.
 - [79] Nobuo Kawabata and Takayuki Mori. Disambiguating ambiguous figures by a model of selective attention. *Biological Cybernetics*, Vol. 67, No. 5, pp. 417–425, 1992.
 - [80] Jannis Wernery, Harald Atmanspacher, Jürgen Kornmeier, Victor Candia, Gerd Folkers, and Marc Wittmann. Temporal processing in bistable perception of the necker cube. *Perception*, Vol. 44, No. 2, pp. 157–168, 2015.
 - [81] Ming Meng and Frank Tong. Can attention selectively bias bistable perception? differences between binocular rivalry and ambiguous figures. *Journal of vision*, Vol. 4, No. 7, pp. 2–2, 2004.
 - [82] Bruno Laeng, Sylvain Sirois, and Gustaf Gredebäck. Pupillometry: A window to the preconscious? *Perspectives on psychological science*, Vol. 7, No. 1, pp. 18–27, 2012.
 - [83] Daniel Kahneman. *Attention and effort*, Vol. 1063. Citeseer, 1973.
 - [84] Eckhard H Hess and James M Polt. Pupil size in relation to mental activity during simple problem-solving. *Science*, Vol. 143, No. 3611, pp. 1190–1192, 1964.
 - [85] Daniel Kahneman and Jackson Beatty. Pupil diameter and load on memory. *Science*, Vol. 154, No. 3756, pp. 1583–1585, 1966.
 - [86] Marcel A Just and Patricia A Carpenter. The intensity dimension of thought: pupillometric indices of sentence processing. *Canadian Journal of Experimental Psychology/Revue canadienne de psychologie expérimentale*, Vol. 47, No. 2, p. 310, 1993.
 - [87] Daniel Strüder and Michael Stadler. Differences in top — down influences on the reversal rate of different categories of reversible figures. *Perception*, Vol. 28, No. 10, pp. 1185–1196, 1999.
 - [88] Thomas C Toppino. Reversible-figure perception: Mechanisms of intentional control. *Perception & psychophysics*, Vol. 65, No. 8, pp. 1285–1295, 2003.
 - [89] Raymond van Ee, LCJ Van Dam, and GJ Brouwer. Voluntary control and the dynamics of perceptual bi-stability. *Vision research*, Vol. 45, No. 1, pp. 41–55, 2005.
 - [90] Loes CJ van Dam and Raymond van Ee. The role of saccades in exerting voluntary control in perceptual and binocular rivalry. *Vision research*, Vol. 46, No. 6-7, pp. 787–799, 2006.
 - [91] Wolfgang Einhäuser, Kevan AC Martin, and Peter König. Are switches in perception

- of the necker cube related to eye position? *European Journal of Neuroscience*, Vol. 20, No. 10, pp. 2811–2818, 2004.
- [92] Sanae Yoshimoto, Hisato Imai, Makio Kashino, and Tatsuto Takeuchi. Pupil response and the subliminal mere exposure effect. *PloS one*, Vol. 9, No. 2, p. e90670, 2014.
- [93] Jean-Michel Hupé, Cédric Lamirel, and Jean Lorenceau. Pupil dynamics during bistable motion perception. *Journal of vision*, Vol. 9, No. 7, pp. 10–10, 2009.
- [94] Franz Faul, Edgar Erdfelder, Albert-Georg Lang, and Axel Buchner. G* power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior research methods*, Vol. 39, No. 2, pp. 175–191, 2007.
- [95] Open Science Collaboration, et al. Estimating the reproducibility of psychological science. *Science*, Vol. 349, No. 6251, p. aac4716, 2015.
- [96] Yoav Benjamini and Yosef Hochberg. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal statistical society: series B (Methodological)*, Vol. 57, No. 1, pp. 289–300, 1995.
- [97] CJ Ellis. The pupillary light reflex in normal subjects. *British Journal of Ophthalmology*, Vol. 65, No. 11, pp. 754–759, 1981.
- [98] Michael Peters and Philip Servos. Performance of subgroups of left-handers and right-handers. *Canadian Journal of Psychology/Revue canadienne de psychologie*, Vol. 43, No. 3, p. 341, 1989.
- [99] Asher Koriath and Joel Norman. Mental rotation and visual familiarity. *Perception & Psychophysics*, Vol. 37, No. 5, pp. 429–439, 1985.
- [100] Heinrich R Liesefeld and Hubert D Zimmer. The advantage of mentally rotating clockwise. *Brain and cognition*, Vol. 75, No. 2, pp. 101–110, 2011.
- [101] J-M Hupé, C Lamirel, and J Lorenceau. Pupil dilation does not predict subsequent stability in perceptual rivalry. *Proceedings of the National Academy of Sciences*, Vol. 105, No. 28, pp. E43–E43, 2008.
- [102] Niels A Kloosterman, Thomas Meindertsma, Anouk M van Loon, Victor AF Lamme, Yoram S Bonne, and Tobias H Donner. Pupil size tracks perceptual content and surprise. *European Journal of Neuroscience*, Vol. 41, No. 8, pp. 1068–1078, 2015.
- [103] B Wilhelm, H Wilhelm, and H Lüdtke. Pupillography: Principles and applications in basic and clinical research. *Pupillography: Principles, methods and applications*, pp. 1–11, 1999.
- [104] Sebastien Bouret and Susan J Sara. Network reset: a simplified overarching theory of locus

- coeruleus noradrenaline function. *Trends in neurosciences*, Vol. 28, No. 11, pp. 574–582, 2005.
- [105] Stephen L Foote and John H Morrison. Extrathalamic modulation of cortical function. *Annual review of neuroscience*, Vol. 10, No. 1, pp. 67–95, 1987.
- [106] Keith A Schneider and Sabine Kastner. Effects of sustained spatial attention in the human lateral geniculate nucleus and superior colliculus. *Journal of Neuroscience*, Vol. 29, No. 6, pp. 1784–1795, 2009.
- [107] Siddhartha Joshi, Yin Li, Rishi M Kalwani, and Joshua I Gold. Relationships between pupil diameter and neuronal activity in the locus coeruleus, colliculi, and cingulate cortex. *Neuron*, Vol. 89, No. 1, pp. 221–234, 2016.
- [108] J Rajkowski. Correlations between locus coeruleus (lc) neural activity, pupil diameter and behavior in monkey support a role of lc in attention. *Soc. Neurosc., Abstract, Washington, DC, 1993*, 1993.
- [109] Michael C Koss. Pupillary dilation as an index of central nervous system $\alpha 2$ -adrenoceptor activation. *Journal of pharmacological methods*, Vol. 15, No. 1, pp. 1–19, 1986.
- [110] MA Phillips, P Bitsios, E Szabadi, and CM Bradshaw. Comparison of the antidepressants reboxetine, fluvoxamine and amitriptyline upon spontaneous pupillary fluctuations in healthy human volunteers. *Psychopharmacology*, Vol. 149, No. 1, pp. 72–76, 2000.
- [111] Dag Alnæs, Markus Handal Sneve, Thomas Espeseth, Tor Endestad, Steven Harry Pieter van de Pavert, and Bruno Laeng. Pupil size signals mental effort deployed during multiple object tracking and predicts brain activity in the dorsal attention network and the locus coeruleus. *Journal of vision*, Vol. 14, No. 4, pp. 1–1, 2014.
- [112] Daniel Kersten, Pascal Mamassian, and Alan Yuille. Object perception as bayesian inference. *Annu. Rev. Psychol.*, Vol. 55, pp. 271–304, 2004.
- [113] David C Knill and Alexandre Pouget. The bayesian brain: the role of uncertainty in neural coding and computation. *TRENDS in Neurosciences*, Vol. 27, No. 12, pp. 712–719, 2004.
- [114] Ahna R Girshick, Michael S Landy, and Eero P Simoncelli. Cardinal rules: visual orientation perception reflects knowledge of environmental statistics. *Nature neuroscience*, Vol. 14, No. 7, p. 926, 2011.
- [115] Horace Barlow. The exploitation of regularities in the environment by the brain. *Behavioral and Brain Sciences*, Vol. 24, No. 4, pp. 602–607, 2001.
- [116] Mehrdad Jazayeri and J Anthony Movshon. Optimal representation of sensory information

- by neural populations. *Nature neuroscience*, Vol. 9, No. 5, p. 690, 2006.
- [117] Yair Weiss, Eero P Simoncelli, and Edward H Adelson. Motion illusions as optimal percepts. *Nature neuroscience*, Vol. 5, No. 6, p. 598, 2002.
- [118] Xue Zhang, Qian Xu, Yi Jiang, and Ying Wang. The interaction of perceptual biases in bistable perception. *Scientific reports*, Vol. 7, p. 42018, 2017.
- [119] Jürgen Kornmeier, Rike Wörner, Andreas Riedel, and Ludger Tebartz van Elst. A different view on the necker cube - differences in multistable perception dynamics between asperger and non-asperger observers. *PloS one*, Vol. 12, No. 12, p. e0189197, 2017.
- [120] Hermann Von Helmholtz. *Helmholtz's treatise on physiological optics*, Vol. 3. Optical Society of America, 1925.
- [121] Jennifer Sun and Pietro Perona. Where is the sun? *Nature neuroscience*, Vol. 1, No. 3, pp. 183–184, 1998.
- [122] Justin L Gardner. Optimality and heuristics in perceptual neuroscience. *Nature neuroscience*, Vol. 22, No. 4, pp. 514–523, 2019.
- [123] James Jerome Gibson and Leonard Carmichael. *The senses considered as perceptual systems*, Vol. 2. Houghton Mifflin Boston, 1966.
- [124] Liu Zhou, Chenglong Deng, Teng Leng Ooi, and Zijiang J He. Attention modulates perception of visual space. *Nature human behaviour*, Vol. 1, No. 1, pp. 1–5, 2016.
- [125] Atsuki Higashiyama and Kohei Adachi. Perceived size and perceived distance of targets viewed from between the legs: Evidence for proprioceptive theory. *Vision research*, Vol. 46, No. 23, pp. 3961–3976, 2006.
- [126] Atsuki Higashiyama and Miyuki Toga. Brightness and image definition of pictures viewed from between the legs. *Attention, Perception, & Psychophysics*, Vol. 73, No. 1, pp. 144–159, 2011.
- [127] Gunnar Blohm, Aarlenne Z Khan, Lei Ren, Kai M Schreiber, and J Douglas Crawford. Depth estimation from retinal disparity requires eye and head orientation signals. *Journal of vision*, Vol. 8, No. 16, pp. 3–3, 2008.
- [128] Laurence R Harris and Charles Mander. Perceived distance depends on the orientation of both the body and the visual environment. *Journal of vision*, Vol. 14, No. 12, pp. 17–17, 2014.
- [129] Roberto Arrighi, Fortunato Tito Arecchi, Alessandro Farini, and Carolina Gheri. Cueing the interpretation of a necker cube: A way to inspect fundamental cognitive processes.

- Cognitive processing*, Vol. 10, No. 1, pp. 95–99, 2009.
- [130] Iseult AM Beets, F Rösler, DYP Henriques, W Einhäuser, K Fiehler, et al. Online action-to-perception transfer: Only percept-dependent action affects perception. *Vision research*, Vol. 50, No. 24, pp. 2633–2641, 2010.
 - [131] Fumiaki Sato, Bruno Laeng, Shigeki Nakauchi, and Tetsuto Minami. Cueing the necker cube: Pupil dilation reflects the viewing-from-above constraint in bistable perception. *Journal of vision*, Vol. 20, No. 4, pp. 7–7, 2020.
 - [132] Jacob Westfall. Pangea: Power analysis for general anova designs. *Unpublished manuscript*. Available at <http://jakewestfall.org/publications/pangea.pdf>, 2015.
 - [133] Makiko Kouchi and Masaaki Mochimaru. Anthropometric database of japanese head 2001. *National Institute of Advanced Industrial Science and Technology*, pp. H16PRO–212, 2008.
 - [134] H Chris Dijkerman and Edward HF De Haan. Somatosensory processing subserving perception and action: Dissociations, interactions, and integration. *Behavioral and brain sciences*, Vol. 30, No. 2, pp. 224–230, 2007.
 - [135] Andro Zangaladze, Charles M Epstein, Scott T Grafton, and Krish Sathian. Involvement of visual cortex in tactile discrimination of orientation. *Nature*, Vol. 401, No. 6753, pp. 587–590, 1999.
 - [136] Gary Aston-Jones and Jonathan D Cohen. An integrative theory of locus coeruleus-norepinephrine function: adaptive gain and optimal performance. *Annu. Rev. Neurosci.*, Vol. 28, pp. 403–450, 2005.
 - [137] Sebastiaan Mathôt. Pupillometry: psychology, physiology, and function. *Journal of Cognition*, Vol. 1, No. 1, 2018.
 - [138] O Pompeiano, Diego Manzoni, CD Barnes, G Stampacchia, and Paola D’ascanio. Responses of locus coeruleus and subcoeruleus neurons to sinusoidal stimulation of labyrinth receptors. *Neuroscience*, Vol. 35, No. 2, pp. 227–248, 1990.
 - [139] Suetaka Nishiike, Shoji Nakamura, Shiroh Arakawa, Noriaki Takeda, and Takeshi Kubo. Gabaergic inhibitory response of locus coeruleus neurons to caloric vestibular stimulation in rats. *Brain research*, Vol. 712, No. 1, pp. 84–94, 1996.
 - [140] Klaas Bombeke, Wout Duthoo, Sven C Mueller, Jens-Max Hopf, and C Nico Boehler. Pupil size directly modulates the feedforward response in human primary visual cortex independently of attention. *NeuroImage*, Vol. 127, pp. 67–73, 2016.
 - [141] Kenith V Sobel and Randolph Blake. How context influences predominance during binoc-

- ular rivalry. *Perception*, Vol. 31, No. 7, pp. 813–824, 2002.
- [142] Bert Hoeks and Willem JM Levelt. Pupillary dilation as a measure of attention: A quantitative system analysis. *Behavior Research Methods, Instruments, & Computers*, Vol. 25, No. 1, pp. 16–26, 1993.
- [143] Guohua Shen, Kshitij Dwivedi, Kei Majima, Tomoyasu Horikawa, and Yukiyasu Kamitani. End-to-end deep image reconstruction from human brain activity. *Frontiers in Computational Neuroscience*, p. 21, 2019.