Behaviors maintaining perceptual continuity

Lau, Wee Kiat

2020

Lau, W. K. (2020). Behaviors maintaining perceptual continuity. Doctoral thesis, Nanyang Technological University, Singapore.

<https://hdl.handle.net/10356/144248>

<https://doi.org/10.32657/10356/144248>

This work is licensed under a Creative Commons Attribution-NonCommercial 4.0 International License (CC BY-NC 4.0).

Downloaded on 26 Apr 2023 21:39:47 SGT

BEHAVIORS MAINTAINING PERCEPTUAL CONTINUITY

LAU WEE KIAT
SCHOOL OF SOCIAL SCIENCES

2020

BEHAVIORS MAINTAINING PERCEPTUAL CONTINUITY

LAU WEE KIAT

SCHOOL OF SOCIAL SCIENCES

A thesis submitted to the Nanyang Technological University
in partial fulfilment of the requirement for the degree of
Doctor of Philosophy

2020

Statement of Originality

I certify that all work submitted for this thesis is my original work. I declare that no other person's work has been used without due acknowledgement. Except where it is clearly stated that I have used some of this material elsewhere, this work has not been presented by me for assessment in any other institution or University. I certify that the data collected for this project are authentic and the investigations were conducted in accordance with the ethics policies and integrity standards of Nanyang Technological University and that the research data are presented honestly and without prejudice.

14 April 2020

Date

.....

.....
Lau Wee Kiat

Supervisor Declaration Statement

I have reviewed the content of this thesis and to the best of my knowledge, it does not contain plagiarised materials. The presentation style is also consistent with what is expected of the degree awarded. To the best of my knowledge, the research and writing are those of the candidate except as acknowledged in the Author Attribution Statement. I confirm that the investigations were conducted in accordance with the ethics policies and integrity standards of Nanyang Technological University and that the research data are presented honestly and without prejudice.

14 April 2020
Date

Gerrit Maus

Authorship Attribution Statement

This thesis contains material from 2 paper(s) published in the following peer-reviewed journal(s) / from papers accepted at conferences in which I am listed as an author.

Experiments 1.4 – 1.6 is published as Lau, W. K., & Maus, G. W. (2019). Visual serial dependence in an audiovisual stimulus. *Journal of vision*, 19(3), 20-20, <https://doi.org/10.1167/19.13.20>

The contributions of the co-authors are as follows:

- Prof Gerrit Maus revised the manuscript drafts.
- I wrote the manuscript drafts, collected the data, and analyzed the data.

Experiments 2.3 – 2.4 is published as Lau, W. K., & Maus, G. W. (2019). Directional biases for blink adaptation in voluntary and reflexive eye blinks. *Journal of vision*, 19(3), 13-13, <https://doi.org/10.1167/19.3.13>

The contributions of the co-authors are as follows:

- Prof Gerrit Maus provided the initial direction for the experiment and revised the manuscript drafts.
- I wrote the manuscript drafts, collected the data, and analyzed the data.

14 April 2020
Date

.....

Lau Wee Kiat

Acknowledgements

I would like to thank my boss, Dr. Gerrit Maus, for giving me the opportunity to be a PhD student. This has been a gruelling journey, and I am very glad it is finally coming to an end. I thank him for his patience and his guidance in helping me to become a scientist. I also thank him for the opportunities that he has given me, such as the collaboration with Dr. Therese Collins, in Université Paris Descartes, France. With that said, I want to thank the collaborators, Dr. Therese Collins, for her insights, comments, and suggestions for all things related to saccades. I had a blast working in her lab. I want to mention the lab technician, Dr. Hamdi Habacha. Without him, I would be very lost in the world of French. I want to thank him for his support, helping me with translations, as well as being a friend in times of need.

I also cannot forget about my TAC members, Dr. Hong Xu, and Dr. Brown Hsieh for agreeing to be on my committee, their aid, and their time. Their comments were especially important to help kick start my PhD journey from the very beginning. Thanks to the examiners for agreeing to review and critique this thesis, and to consider it good enough for the scientific community. Thanks for taking the time to read through many pages of text in your already very busy schedule.

Last, but not least, I want to thank others who have helped me in my journey: KP (thanks for your insights), Millán Reinares (por todo el mundo te doy mis gracias, y conozcamos muy pronto!!!), colleagues, other professors, and the administrators who are involved since the beginning – admissions, administrative work, examinations, etc. Thank you all for your time and effort.

TABLE OF CONTENTS	Page
Abstract	21–22
Introduction	
0.1.0: Introduction	23
0.1.1: Definition of perception	23
0.1.2: Definition of continuity	23–24
0.1.3: Definition of perceptual continuity	24
0.2.1: Current perspectives of perceptual continuity: hysteresis	24–25
0.2.2: Current perspectives of perceptual continuity: object updating	25–26
0.2.3: Current perspectives of perceptual continuity: temporal stability	27–28
0.2.4: Comparisons between the three perspectives of perceptual continuity	28–29
0.3.0: Issues with current perspectives and the motivation behind the thesis	29–30
0.3.1: Comparing information in the same and different modalities	30
0.3.1.1: Thesis part 1 investigates serial dependence	31
0.3.2: Comparing across endogenously elicited disruptions during blinks	31–32
0.3.2.1: Thesis part 2 investigates gaze changes in blink adaptation	32
0.3.3: Comparing endogenous disruptions in parts of the oculomotor system	33
0.3.3.1: Thesis part 3 investigates saccade planning and blinking	33–34
0.4.0: Important considerations regarding the thesis	34
0.4.1: Premise of testing, assumptions, and cautions for the reader	34–35
0.4.2.1: Further cautions for the reader	35–36
Part 1	
Comparing information in the same and different modalities	
1.0.0: Is temporal stability the same as serial effects in perception?	37

TABLE OF CONTENTS	Page
1.0.1: What are serial effects	37
1.0.1.1: Attractive serial effects	38
1.0.1.2: Repulsive serial effects	38–39
1.0.2: Adaptation is not serial effect	39
1.0.2.1: Priming is not serial effect	39–40
1.0.2.2: Serial effects differ from adaptation and priming	40–41
1.0.3: Revisiting if temporal stability is an expression of serial effects	41
1.0.3.1: Serial dependence definition and how it works	41–42
1.0.3.2: Serial dependence in cell population processing	42
1.0.3.3: Serial dependence as working memory	42
1.0.3.4: Serial dependence as responses to uncertainty	42–43
1.0.4: Serial dependence as an expression of temporal stability	43
1.0.4.1: Serial dependence is evident in vision studies but limited in audition	44
1.1.0: Experiment 1.1 investigates serial dependence for pitch	44
Methods	
1.1.1: Participants are musicians	44–45
1.1.2: Apparatus	45
1.1.2.1: Stimulus are two sets of pitch an octave below the other	45–46
1.1.3: Procedure	46–47
1.1.4: Analysis and general descriptions	47
1.1.4.1: Quantifying serial dependence by curve fitting	48
1.1.4.2: Fixed effects analysis to measure serial dependence at the group level	48
1.1.4.3: Simulations	48

TABLE OF CONTENTS	Page
Results	
1.1.5: Descriptive statistics and individual data	49–50
1.1.5.1: Fixed effects analysis show no serial dependence and simulation found artifacts	50–51
1.2.0: Experiment 1.2 investigates serial dependence for auditory locations	51
Methods	
1.2.1: Participants did not require musical expertise	52
1.2.2: Apparatus	52
1.2.2.1: Stimulus are tone locations using interaural differences	52–53
1.2.3: Procedure	54
1.2.4: Identical analysis to experiment 1.1	54–55
Results	
1.2.5: Descriptive statistics and individual data	55–56
1.2.5.1: Fixed effects analysis showed no serial dependence and simulations found artifacts	56–57
Discussion	
1.2.6: Inconclusive results for experiment 1.1 and 1.2 due to artifacts	57–58
1.2.6.1: Edge artifacts from a linear stimulus space confounded serial dependence analysis	58–59
1.2.6.2: Edge artifacts do not disappear by omitting data from extremities	59–60
1.2.6.3: Linear stimulus space causes artifacts	60–61
1.2.6.4: Central tendency bias when responding to auditory positions	61–62
1.2.6.5: Criticisms of current methods to determine auditory locations	62
1.2.6.6: Fixation and lateralization effects	62–63
1.2.7: Semantic information and the concept of circular space	63–64

TABLE OF CONTENTS	Page
1.3.0: Experiment 1.3 investigates auditory serial dependence in vowels	64
Methods	
1.3.1: Participants	65
1.3.2: Apparatus	65
1.3.2.1: Stimulus	65–66
1.3.2.2: Vowel synthesis and auditory noise	66–68
1.3.3 Procedure	68–69
1.3.4: Analysis for serial dependence	69
1.3.4.1: Permutations for significance testing and confidence intervals	69–70
Results	
1.3.5: Descriptive statistics	70–71
1.3.5.1: Individual response errors	71–73
1.3.5.2: Fixed effects analysis results	73–74
Discussion	
1.3.6: Experiment 1.3 did not find serial dependence in vowels	74–75
1.3.6.1: Vowel boundaries, prototypes, and its role in vowel discrimination	75–76
1.3.6.2: Serial dependence is evident in categorical face perception	76–77
1.3.6.3: Awkward vowel morph steps	77–78
1.4.0: Is serial dependence perceptual or decision?	78–79
1.4.0.1: Testing if serial dependence is perceptual or decision with a multimodal stimulus	79–80
1.4.0.2: Experiments 1.4–1.6 test serial dependence using a multimodal stimulus	80–81
Methods	
1.4.1: Participants	81

TABLE OF CONTENTS	Page
1.4.2: Apparatus	82
1.4.2.1: Stimulus	82–85
1.4.3: Procedure for experiment 1.4	85
1.4.3.1: Procedure for experiment 1.5	85–86
1.4.3.2: Procedure for experiment 1.6	86
1.4.4: Analysis and general descriptions	86–87
1.4.4.1: Means-subtraction and raw-subtraction descriptions	87–88
1.4.4.2: Serial dependence analysis	88
1.4.4.3: Fixed effects analysis and hypothesis testing	88–89
Results	
1.4.5: Descriptive statistics	89–92
1.4.5.1: Experiment 1.4 means-subtraction shows visual but not auditory serial dependence	92–95
1.4.5.2: Experiment 1.4 raw-subtraction shows visual but not auditory serial dependence	95–97
1.4.5.3: Experiment 1.5 means-subtraction show visual serial dependence within and across modalities	97–98
1.4.5.4: Experiment 1.5 raw-subtraction show visual serial dependence within and across modalities	99–100
1.4.5.5: Experiment 1.6 means-subtraction show serial dependence without responses	100–102
1.4.5.6: Experiment 1.6 raw-subtraction shows serial dependence without responses	102–105
1.4.5.7: Evaluating the bias subtraction methods	105
Discussion	
1.4.6: Visual serial dependence in a multimodal stimulus even when task expectations are violated	106
1.4.6.1: Serial dependence, an effect of perceiving the previous stimulus	107–108

TABLE OF CONTENTS	Page
1.4.6.2: Serial dependence and multimodal integration	108–109
1.4.6.3: Lack of auditory serial dependence	109–110
1.4.6.4: Timing is important for auditory serial dependence	110–111
1.4.6.5: Auditory serial dependence may be linked to working memory	111
1.4.6.6: Serial dependence and inconsistent analysis	111–112
1.4.6.7: Serial dependence and the natural environment	112–113
1.4.6.8: Interim summary	113–114
 General discussion for part 1	
1.5.0: Sample size differences across serial dependence studies and the expected effect sizes and confidence intervals	115–116
1.5.1: Results for expected effect sizes and confidence intervals	116
1.5.2: Serial dependence as a functional unit of temporal stability	116–117
1.5.3: Temporal stability is modality-specific, less so a serial effect	117–118
Part 1 conclusion	118–119
 Part 2	
Comparing across endogenously elicited disruptions during blinks	
2.0.0: Introduction to part 2	120–121
2.0.1: Physiological reasons for blinking	121–122
2.0.1.1: Blinking and the brain	122–123
2.0.2: Eye blinks and perceptual continuity	123
2.0.2.1: Visual suppression during blinking	124–125
2.0.3: Change blindness in perceptual continuity	125
2.0.3.1: Awareness in change blindness and controversies	125–126
2.0.3.2: Theories that explain why we are blind to change	126–129
2.0.4: Position change detection and blink adaptation	129–130

TABLE OF CONTENTS	Page
2.0.5: Investigating blink adaptation	130–131
2.1.0: Experiment 2.1 and 2.2 investigates blink adaptation using voluntary and reflexive blinks	131
Methods	
2.1.1: Participants	131–132
2.1.2: Stimulus and apparatus	132–133
2.1.3: Procedure for both experiments	134
2.1.3.1: Experiment 2.2. air puff details	134–135
2.1.3.2: Experiment 2.2. air puff training	135–136
2.1.4.1: Analysis for gaze calculations	136–137
2.1.4.2: Analysis for time-course	137
2.1.4.3: Analysis for blink adaptation	138–139
Results	
2.1.5.1: Experiment 2.1	139–141
2.1.5.2: Experiment 2.2	141–143
Discussion	
2.1.6: Not enough evidence to suggest blink adaptation	143–144
2.1.6.1: The two significant results	144–145
2.1.6.2: The lack of a baseline	145
2.2.0: Motivation for experiments 2.3 and 2.4	145–146
2.2.0.1: Experiment 2.3 tests larger displacements, and experiment 2.4 tests for binocular adaptation	146–147
Methods	
2.2.1: Participants	147
2.2.2: Stimulus and apparatus	147–149

TABLE OF CONTENTS	Page
2.2.3.1: Procedure – experiment 2.3	149–150
2.2.3.2: Procedure – experiment 2.4	150–151
2.2.4.1: Analysis – gaze calculation	151
2.2.4.2: Analysis for time-course	151–152
2.2.4.3: Analysis for single trial data in one participant	152
2.2.4.4: Analysis for blink adaptation	152–154
Results	
2.2.5.1: Experiment 2.3	154–157
2.2.5.2: Experiment 2.4	157–160
Discussion	
2.2.6: Blink adaptation occurs in all directions and in both eyes	160
2.2.6.1: Adaptation magnitude is unequal across directions	160–162
2.2.6.2: Possible adaptation in reflexive blinks	162–163
2.2.6.3: Binocular differences in blink adaptation	163–164
2.2.6.4: Saccadic and blink adaptation	164
2.2.6.5: Does blink adaptation maintain perceptual continuity?	164–165
2.2.6.6: Interim summary	165–166
General discussion for part 2	
2.3.0: Expected effect sizes and confidence intervals between our study and existing studies	166
2.3.1: Results for expected effect sizes and confidence intervals	167
2.3.2: Revisiting whether modality-specific temporal stability is a failure of change detection	167–169
2.3.3: Temporal stability is reached by recruiting systems to ensure stability	169–170
Part 2 conclusion	170–171

TABLE OF CONTENTS**Page****Part 3****Comparing endogenous disruptions in parts of the oculomotor system**

3.0.0: Introduction to part 3	172–173
3.0.1: The nature of saccades	173–174
3.0.2: Saccade classifications	174–176
3.0.3: Saccades: from intention to movement	176–177
3.0.4: Saccades and perceptual continuity	177–179
3.0.5: How saccades relate to blinks	179–180
3.0.6: The corollary discharge, motor plans and updating	180–182
3.1.0: Saccade planning and blinks	182–183
3.1.0.1: Experiment 3.1 tests saccade planning when blinks occur, and if fixational errors predict saccade accuracy	183–184

Methods

3.1.1 Participants	184–185
3.1.2: Apparatus	185
3.1.2.1: Stimulus and trial sequence	185–187
3.1.3: Procedure	187–189
3.1.4: Gaze position analysis	189–190
3.1.4.1: Fixation errors analysis	190–191
3.1.4.2: Statistical analysis software and descriptive statistics	191–192
3.1.4.3: Linear mixed model to investigate blinks and saccade planning	192–194
3.1.4.4: Before-saccade errors comparison and rationale	194
3.1.4.5: Stepwise regression investigates fixation errors on saccade planning	195
3.1.4.6: Tracker drift and systematic bias analysis	195–196

TABLE OF CONTENTS	Page
Results	
3.1.5: Descriptive statistics for horizontal amplitudes and landing errors	196
3.1.5.1: Descriptive statistics for vertical amplitudes and landing errors	196–198
3.1.5.2: Descriptive statistics for oblique amplitudes and summary	198
3.1.5.3: LMM estimating landing errors	198–201
3.1.5.4: Before-saccade errors	202–205
3.1.5.5: Stepwise regression evaluates which before-saccade errors predicted saccade landing errors	205–209
3.1.5.6: Time-course analysis	209–211
Discussion	
3.1.6: Saccade plan updates after the blink and saccade accuracy is predicted by events after blinking	211–212
3.1.6.1: Saccade planning and blinking	212–214
3.1.6.2: Blinking and saccade landing errors	214–215
3.1.6.3: Specific fixational errors are involved in saccade planning	215–217
3.1.6.4: Saccade planning and the real world	218
3.1.6.5: Interim summary	218–219
General discussion for part 3	
3.2.0: There is a signal which anticipates eye positions after blinking	220–221
3.2.1: The signal after blinking which updates saccade plans in relation to existing perspectives	221–222
Part 3 conclusion	222–223
General discussion for thesis	
4.1: Temporal stability based on this thesis	224–225
4.2: Shortcomings of this thesis and suggestions	225–227
4.3: What remains unanswered?	227–228

TABLE OF CONTENTS	Page
Thesis conclusion	
Behaviors could maintain perceptual continuity	228–230
References	231–249

LIST OF FIGURES	Page
Figure 1.1.1	46
Figure 1.1.2	49
Figure 1.1.3	50
Figure 1.1.4	51
Figure 1.2.1	53
Figure 1.2.2	55
Figure 1.2.3	56
Figure 1.2.4	57
Figure 1.2.5	58
Figure 1.2.6	59
Figure 1.2.7	60
Figure 1.3.1	66
Figure 1.3.2	67
Figure 1.3.3	71
Figure 1.3.4	72
Figure 1.3.5	72
Figure 1.3.6	73
Figure 1.3.7	74
Figure 1.4.1	83
Figure 1.4.2	90
Figure 1.4.2.1	91
Figure 1.4.3	94
Figure 1.4.3.1	96
Figure 1.4.4	98

LIST OF FIGURES	Page
Figure 1.4.4.1	100
Figure 1.4.5	102
Figure 1.4.5.1	104
Figure 2.1.1	133
Figure 2.1.2	139
Figure 2.1.3	140
Figure 2.1.4	141
Figure 2.1.5	142
Figure 2.2.1	148
Figure 2.2.2	153
Figure 2.2.3	156
Figure 2.2.4	156
Figure 2.2.5	157
Figure 2.2.6	159
Figure 3.0.1	174
Figure 3.1.1	186
Figure 3.1.2	197
Figure 3.1.3	199
Figure 3.1.4	202
Figure 3.1.5	204
Figure 3.1.6	210
Figure 3.1.7	210
Figure 3.1.8	211

LIST OF TABLES	Page
Table 1.3.1	74
Table 1.4.1	93
Table 1.4.1.1	95
Table 1.4.2	97
Table 1.4.2.1	99
Table 1.4.3	101
Table 1.4.3.1	103
Table 1.5	116
Table 2.1	167
Table 3.1.1	200
Table 3.1.2	201
Table 3.1.3	207
Table 3.1.4	208

Abstract

Our perception of the world is continuous although the input to various senses is fraught with perturbations and ambiguities. Perceptual continuity is defined as the continuous experience of external, discriminable things which involves some implicit reasoning to complete missing information. In this thesis, we conducted psychophysical experiments to investigate behaviors that maintain perceptual continuity over three parts.

In Part 1, we investigated response behaviors. Responses to a stimulus do not deviate from each other if the stimulus appeared stable and non-changing. We examined response behaviors through serial dependence. Serial dependence is an effect in which the current response error is biased by the preceding stimulus. We showed that our responses to visual stimulus can be biased (i.e. assimilate) to similar or stable objects. In the case of serial dependence, our responses to the physical world appear to be embedded in perception, and we become biased by what we previously perceived.

In Part 2, we investigated how observers behaved if they were unaware to consistent changes. We do not notice changes which occur during eye blinks because of missing visual information. We introduced a dot stimulus which steps repeatedly during the blink and showed that the oculomotor system adapted to positional changes across blinks even though the observers were unaware of the changes. From this, we deduced that the oculomotor system could maintain perceptual continuity by blink adaptation behaviors: positional changes were minimized during the blink. Therefore, objects appear to be in the same position after the blink. Since the object appears to not have changed, the perception of the object's position remains continuous.

In Part 3, we studied how saccade planning is influenced by blinks and fixation errors. The oculomotor system plans the saccade before shifting our eyes to where we want them to. The saccade plan is updated when additional movements occur. This updating allows the oculomotor system to ensure our eyes land accurately at the destination. We asked if the saccade plan was also updated simply by blinking, since the eyes move during the blink. We found that saccades to visible objects were more accurate if observers blinked after saccade planning. This indicated that saccade plans were updated to enable a continuous experience of visual exploration because our eyes land where we want them to.

In summary, this thesis addressed the following behaviors that could maintain perceptual continuity: 1) through serial dependence, we continue to respond in a similar way based on what we saw previously, 2) positional changes of a target are minimized across a blink, and 3) saccade plans are updated when we blink during visual exploration to visible targets. We then argued that these findings help explain how temporal stability ensures perception is continuous. Temporal stability may be achieved by expressing serial dependence which may be limited to vision. Within vision, temporal stability is not only a failure of change detection. Stability is achieved by recruiting the oculomotor system. The oculomotor system then uses a signal that anticipates eye positions after blinking to re-orient our eyes during blinks, or to update the saccade plans so that that our eyes land on the target.

Perceptual Continuity

0.1.0: Introduction

The world we experience is continuous and stable. Even though sensory information is often disrupted, such as through blinks, or constantly changing, such as when objects are in motion, we do not perceive the disruptions, nor do we treat the objects as novel after each change. But what makes our perception of the world stable? Let us first define perception and continuity.

0.1.1: Definition of perception

According to R. Efron (1969), perception is the “direct, immediate awareness of discriminated existents which results from patterns of energy absorption by groups of receptors” (pp. 147). The term *discriminated existents* refers to external things which exist and can be discriminated, isolated, and separated from others. Humans do not perceive discrete energy quanta. Instead, the patterns are perceived in gradients. These gradients are the physical pre-condition for us to experience the world. If there were no gradients acting on sensory receptors, our perception becomes undifferentiated and homogenous because there is nothing to separate. Hence, perception is the observer’s experience to external, discriminable things.

0.1.2: Definition of continuity

Continuity was first investigated by Gestalt psychologists in perceptual organization such as *Amodal Completion* (Kanizsa, 1979). Basically, an object partly hidden by an opaque surface appears complete, *continuing* behind the surface, even though we do not see the full object (Gerbino & Salmaso, 1987). Completion is possible because it is partly a mental process based on logic and reasoning about the object. However, completion is sometimes irrational because “in ... a situation in which sensory input is absent, the visual system is *free* to choose the form of

continuation” (Kanizsa, 1985, p. 29). This means that the completion (i.e. continuation) of an occluded object does not have to be veridical if it makes sense to the observer. Therefore, continuity is the continuation of information that is meaningful to the observer even though part of the information (from sensory signals) is momentarily lost.

0.1.3: Definition of perceptual continuity

In this thesis, perception is the experience of external, discriminable objects. When sensory signals are momentarily lost, perception is continued to complete the missing information. Continuity involves a mental and conscious process in which logic and reasoning is used to fill-in missing information. The percept that is completed need not match the sensory signals as if the signals were never lost. The continued information must make sense to (or be understood/interpretable by) the observer. Therefore, perceptual continuity is the continuous experience of external, discriminable things which involves the conscious completion of missing information using some form of implicit reasoning that the observer understands. The sensory modalities discussed and tested in the thesis are limited to vision and/or audition.

0.2.1: Current perspectives of perceptual continuity: hysteresis

It is thought that perceptual continuity in vision occurs because of perceptual hysteresis. Perceptual hysteresis is a persistent state in which the current perception is resistant towards new information and what is perceived lags behind actual information (Fender & Julesz, 1967). When hysteresis occurs, an observer finds it difficult to move from the old information to the new because the old information is interfering with new. For example, observers can only see one percept in a multi-stable image, but must look away and back in order to switch to a different percept (Ramachandran & Anstis, 1985). In this case, hysteresis causes a continuous

experience of the percept because newer information cannot immediately change the percept. The percept is only changed when a large amount of new information forces the persistent state to switch percepts.

The persistent state is the result of neurons coordinating within a network in response to stimulation. States are resistant to changes because many neurons within the same network must be stimulated to effect a change in percept (Williams, Phillips, & Sekuler, 1986). This is evident in higher visual processes. For example, cortical activity in the lateral occipital complex and the ventral V4 remained active during hysteresis but not when the hysteresis was absent (Large, Aldcroft, & Vilis, 2005). The lateral occipital complex processes object recognition and mediates object percepts between iconic and short-term memory. Since persistent states occur in the lateral occipital complex, it suggests that persistent states may also be a type of memory (Ferber, Humphrey, & Vilis, 2005). Therefore, hysteresis momentarily preserves the object's percept, leading to a continuous perception of the object.

0.2.2: Current perspectives of perceptual continuity: object updating

Perceptual continuity could be a result of object representation updating. Objects are represented by components in visual processing. Visual features such as depth, motion, and textures are broken into simpler components and processed in parallel (Williams, 1992). These components are reassembled in different cortical regions and we perceive the object based on the combined representations (Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999). Object features are perceived incorrectly when errors occur during reassembly. As a result, some objects appear different than before because the components are mixed up (Humphreys, Duncan, Treisman, & Treisman, 1998). This causes a break in the perceptual continuity of the

object because the features are changed. How does the brain reassemble components correctly to ensure a continuous percept of the object?

Objects may be reassembled, and the percept kept continuous, from object updating (Enns, Lleras, & Moore, 2010). According to this theory, an observer forms meaningful object representations in relation to the scene. During perception, these representations are constantly resampled. Information that do not match existing representations is interpreted as new. Object representations for new items are then formed. Changes to individual features of the object are updated so long as the features belong to an existing object representation. Objects are perceived as continuous because the resampling during perception constantly updates existing representations of each object.

Object updating is demonstrated by visual masking. Visual masks often overlay the visual stimulus to prevent the interference to subsequent visual stimulus (Kahneman, 1968). However, unattended objects can be masked by placing four small dots over the object. In one experiment, object identification accuracies fell drastically when four small dots ($.20^\circ$) appeared 45 ms after an object was presented 3° from the center screen to the periphery. Participants could not always identify individual object features that switched when the dot mask appeared (Enns & Di Lollo, 1997). This study demonstrated object updating because changes to individual features did not result in any improves to object identification. Additional support of object updating came from Moore and Egeth (1997), in which participants were freed from the four dot visual masking if they treated the mask as a separate object. Collectively, these studies provided evidence to support object updating. Object representations are constantly updated to provide a continuous object perception.

0.2.3: Current perspectives of perceptual continuity: temporal stability

Physical changes in the environment can happen and the observer may not notice them. When the observer evaluates the percept before and after the change, and notices nothing, the observer likely considers the percept the same. By this logic, perceptual continuity is a form of temporal stability for unnoticed changes across two evaluation points. Temporal stability is the stability of information over time (Hock, Schöner, & Giese, 2003). Perception to an object remains stable and continuous over time when an object's state is stabilized. An object's state refers to the object's current configuration. This is illustrated in the following study with bistable stimuli and apparent motion. Bistable stimuli are images that elicit two different percepts depending on their current configurations (Gorea & Lorenceau, 1984). Apparent motion occurs when two slightly displaced objects are presented one after the other, and the object appears to be moving continuously (Anstis, MacKay, Longuet-Higgins, & Sutherland, 1980; Yantis & Gibson, 1994).

Hock, Kelso, and Schöner (1993) demonstrated perceptual continuity using bistable images and apparent motion over multiple experiments. The bistable images were alternating black and white squares which elicited horizontal and vertical apparent motions. The experiments varied across stimulus size and alternation speed. Participants were tasked to report the direction they perceived. Hock and colleagues showed that the perceived apparent motion was temporally stable if spontaneous alternations (i.e. sudden change to alternating patterns which elicits a different motion direction) did not occur. Importantly, the more an observer experienced hysteresis, the less temporal stability there was to the current motion percept, causing the observer to perceive spontaneous switching between horizontal and vertical apparent motion.

Therefore, temporal stability allows an observer to hold onto the current percept. In other words, the percept remains continuous over time.

0.2.4: Comparisons between the three perspectives of perceptual continuity

Each of the three perspectives brings a unique way of describing how perception is kept continuous. Hysteresis states the perception is continuous because there is a lag before new information is perceived. Object updating states that individual features are not important because they are constantly updated. Object perception is continuous so long as the object representations exist in the perceptual system. Temporal stability claims that perception is stable over time because the previous and current information is the same. Stability is broken when information is different. These perspectives provide theories for specific instances of perceptual continuity. However, this also results in potential flaws.

Not all perspectives can explain perceptual continuity in a broader sense. Hysteresis seems the briefest. Continuity is immediately broken as soon as new information penetrates the sluggish previous information. This is as quick as looking away and back (Ramachandran & Anstis, 1985). This is problematic for perceptual continuity as perception cannot be continuous when something as simple as looking away and back would break continuity. Object updating is a better exponent for perceptual continuity over hysteresis. An existing object representation that is constantly updated during perceptual sampling creates continuous object perception. Therefore, small changes to an object do not cause it to appear different. Temporal stability appears to be a catch-all definition since perception is continuous when percepts are stable. This explanation works for broadly explaining perceptual continuity. It suffers for more refined examples, such as the type of percept that is compared to.

Some perspectives may share similar mechanisms. For example, hysteresis and object updating are both involved in object perception. Hysteresis is observed in higher visual areas which process objects and object-related memory. This suggests that hysteresis could be a precursor to object updating. For example, when hysteresis causes a lag in the previous percept, this process could be how an object's representation is first formed. Thereafter, object updating constantly updates the representation during perceptual sampling to create continuous object perception. Unfortunately, object updating does not recognize the role of hysteresis.

0.3.0: Issues with current perspectives and the motivation behind the thesis

What is common across the three perspective is that they all involve an evaluation between new and previous information. Specifically, the perceptual system evaluates previous and the current information, and continuity is somehow achieved by hysteresis, object updating, or temporal stability. In the case of hysteresis, the previous information causes perception to be sluggish and perception lags the incoming information. The perceptual system compares the hysteresis to the new information before deciding which percept the observer experiences. The incoming information can be ever-changing. However, it must successfully penetrate the persistence of the hysteresis before the observer can perceive it. Otherwise, the previous percept continues over to the new information.

In object updating, object perception is continuous because of constant updating. Updating is a comparison procedure that determines if incoming information fits existing representations. An object can experience changes to individual features. Individual feature changes do not result in new object representations. They are simply updated if the features belong an existing object representation. If incoming information does not match any present representations, then new representations are

formed. Therefore, the observer perceives the newly represented object continuously at each updating.

The evaluation process for temporal stability is the most problematic. According to the theory, the perceptual system simply evaluates the previous and current information over time. An object is perceptually continuous if the previous percept does not differ from the current, even if physical changes occur. This explanation is too general as compared to those described in hysteresis or object updating. There appears to be no limitations nor boundaries on how the evaluation functions, nor what happens during such comparisons, nor the kind of information that renders a percept continuous. Therefore, our current understanding of temporal stability requires further investigations.

Current research has not provided enough evidence to better refine the definition of temporal stability nor address the limitations and flaws of the theory. Therefore, the purpose of this thesis is to investigate some aspects of temporal stability. The following sections (0.3.1 – 0.3.3) describe the theory's weakness, that, when addressed, would provide refined clarifications to how temporal stability relates to perceptual continuity.

0.3.1: Comparing information in the same and different modalities

According to temporal stability, objects remain continuous when the previous and the current information do not differ. In some sense, this suggests that temporal stability is dependent on previous information before knowing if the current information is stable. Under this assumption, we either combine information or discard some of them to form a perceptually continuous environment. It remains unclear the types of information that gets integrated or discarded. For instance, is information from the same modality integrated, or can integration occur over modalities?

0.3.1.1: Thesis part 1 investigates serial dependence

Part 1 of this thesis investigates Serial dependence. Serial dependence may be a way to integrate current information based on previous information (J. Fischer & Whitney, 2014). Specifically, serial dependence is a bias that occurs when two similar objects are presented sequentially. Our response to the current object becomes influenced by the previous.

Serial dependence is often examined in the visual domain. We tested for serial dependence using different auditory stimuli. However, we did not replicate auditory serial dependence. There is also a current debate whether serial dependence is a perceptual or a decision-making effect. We contributed to this debate by testing serial dependence using a multimodal stimulus. From the multimodal stimulus, we showed that serial dependence is likely a perceptual effect. This indicated that the way we visually interact with the environment could be largely due how we perceive objects in the environment. As such, our visual responses become influenced by what we previously perceived. From this finding, temporal stability could be modality-specific, and it may also involve other mechanisms which help maintain perceptual continuity.

0.3.2: Comparing across endogenously elicited disruptions during blinks

Part 1 of the thesis highlighted the likelihood that temporal stability is modality-specific. Therefore, the remaining thesis limits investigation to the visual domain. The visual environment suffers from endogenously elicited disruptions in the form of eye blinks. We blink about 12–20 times per minute (Bentivoglio et al., 1997; Griepentrog & Lucarelli, 2011; Karson, 1983; Karson et al., 1981). When we blink, the eyelids cover the eye. There is blackness as no visual input is entering the eyes. According to temporal stability, we would constantly experience perceptual discontinuities after every blink because the blackness during the blink already

differed from the percept of the environment from before the blink. Since we do not experience discontinuities, it means that temporal stability cannot be simply explained by a process of comparing previous and current information. For example, it is possible that temporal stability ignores the endogenous changes elicited by blinking. If temporal stability ignores changes from the blink, what happens to the fixation of an object if the object changes position during the blink?

0.3.2.1: Thesis part 2 investigates gaze changes in blink adaptation

Part 2 of this thesis investigates gaze changes during blink adaptation. Blink adaptation occurs when the oculomotor system detects positional changes of an object during the blink, and corrects our gaze by shifting our eyes toward the new object position after blinking (Maus et al., 2017). Could blink adaptation help explain how temporal stability contributes to perceptual continuity?

We tasked participants to look at a fixation dot. The dot was displaced in one of four directions during the blink. Participants, after many trials, adapted to the displaced dot position after the blink. The gaze position after the blink was closer to the displaced dot as compared to a stationary dot. This finding illustrated that blink adaptation shifts our gaze towards positional changes of an object happening during the blink. Positional discrepancies across the blink were minimized and the object's position before and after the blink appeared alike. Therefore, the oculomotor system may be demonstrating behaviors that maintain temporal stability, by ensuring that the position of the current information is as close to the previous as possible. This suggests that temporal stability is not only a failure of change detection, but it requires other systems (i.e. the oculomotor system) to process or guide behaviors to ensure perceptual continuity. We also speculated that there could be a signal after blinking. This signal could be important in temporal stability.

0.3.3: Comparing endogenous disruptions in parts of the oculomotor system

Part 2 showed that temporal stability in vision is attained by recruiting the oculomotor system. We speculated that there could be a signal within the oculomotor system that provides information about where the eye would be after blinking. Could this signal also contribute to temporal stability? In part 3, we expanded this by testing a different arm of the oculomotor system in conjunction with the endogenous disruptions from blinks. Specifically, we investigated temporal stability in saccades disrupted by blinks. Saccades are fast, ballistic movements that we make to explore the visual environment (Becker & Fuchs, 1969). Saccade start positions are affected when we blink before launching the saccade. This is because the eyes do not return to the exact same position after blinking (Collewijn, Van Der Steen, & Steinman, 1985; Riggs, Kelly, Manning, & Moore, 1987). If the start position changes and the oculomotor system does not recompute the computations involved in guiding the saccade to the target, then the saccade would never reach the destination. Since the saccade is already planned, and the observer now makes a new movement by blinking, does the oculomotor system re-plan the saccade?

0.3.3.1: Thesis part 3 investigates saccade planning and blinking

In part 3 of the thesis, we investigated whether saccade plans were updated when irrelevant movements were introduced. Participants either blinked or remain fixated before making saccades to visible targets or remembered target positions. We showed that saccades to visible targets became more accurate after blinking, than when participants only fixated. This indicated that the saccade plans were updated because blinking introduced erroneous movement information to the old saccade plan.

The speculation from part 2 that there could be a blink-related signal which anticipates eye position after blinking was observed in part 3 to help maintain

temporal stability in vision. Particularly, the oculomotor system updated saccade plans to ensure that saccades to visible objects remain accurate after an observer blinked. Saccade plans were updated due to this signal which was created to anticipate eye positions after blinking. This updating ensured that the oculomotor system directed the eyes to where we want to look. Temporal stability in vision was ensured by recruiting the oculomotor system. This involved a signal in the oculomotor system which anticipated eye positions after blinking. The signal then contributed to saccade plan updating to ensure our eyes land accurately. Therefore, we have temporal stability because our eyes arrive at where we want, even after blinking.

0.4.0: Important considerations regarding the thesis

The thesis is structured in three parts followed by a general discussion and summary section. Literature review is conducted separately to address the issues raised pertaining to temporal stability (see 0.3.1 – 0.3.3). Each part begins with an overview of the current literature before going in-depth into the issues surrounding the topic. This thesis investigated the behaviors which could maintain perceptual continuity. The findings were then extrapolated to improve our current understanding of temporal stability. It is important that the reader remembers that the thesis does not implicate perceptual continuity as a solely behavioral process.

0.4.1: Premise of testing, assumptions, and cautions for the reader

The following premise and assumptions are described so that the reader has a better understanding of what to expect for the experiments. Experiments conducted in the thesis were confined to laboratory settings, using psychophysical paradigms. Psychophysics is the study of how sensation is associated to stimuli (Gescheider, 2013). This is an objective measure because a change of X in the stimulus results in a behavioral response of Y. We limited our investigations to visual and auditory

domains based on the questions described in 0.3.1 – 0.3.3. There were no subjective measurements in this thesis. More precisely, we did not evaluate if the environment appeared continuous to the observer, or if the observer noticed/experienced discontinuities. Also, observers refer to healthy human participants. This thesis assumed that objects in the physical world typically do not change abruptly without external influence. For instance, an inanimate object remains unchanged when the object does not receive external interventions. In the next section, we described how we drew conclusions using psychophysical paradigms, and spelled out more cautions for the reader.

0.4.2.1: Further cautions for the reader

We used psychophysical paradigms to test the relationship between stimulus and sense in human participants. For instance, when a stimulus X changes, the observer exhibits behavior Y. We then extrapolated from this observation and speculated how behavior Y could maintain perceptual continuity if stimulus X always changed the same way. This conclusion does not suggest that behavior Y causes perceptual continuity because of the change in stimulus X. Rather, it is an inference about the relationship between stimulus X and behavior Y. This reasoning may unwillingly suggest that perceptual continuity is an exaggerated form of serial processing. However, the thesis does not make this claim.

The focus of this thesis was not to measure parallel processing in perception. It is known that perception involves parallel processing. Multiple perceptual information is processed simultaneously (Nassi & Callaway, 2009). This includes simple features such as orientation (Fahle, 1994), to more complex ones like motion (Favreau, 1976), faces (Martens, Leuthold, & Schweinberger, 2010), and speech (Wood, 1974). Parallel processing may also play a role in maintaining stable perception over time. This thesis

did not investigate parallel processes associated with perception. Psychophysical experiments could be employed to investigate parallel processing. However, this was also not conducted in this thesis and was not the focus of the thesis. Hence, the reader is cautioned when questioning the role of parallel processing in perceptual continuity and temporal stability based on the conclusion in this thesis.

Part 1: Comparing information in the same and different modalities**1.0.0: Is temporal stability the same as serial effects in perception?**

Temporal stability is the stability of information over time (Hock et al., 2003). The perceptual system ensures that perception is continuous when the previous and the current information do not differ over time. One problem with comparing information between previous and current time points is that prior information history influences how the current information is evaluated. Since temporal stability compares previous and current information, it may also be affected by prior information history. History effects are often observed in psychophysical experiments. These effects are called serial effects. We review the literature on serial effects in the next few sections.

1.0.1: What are serial effects

Serial effects are response biases observed when responding to information presented in sequence. They are investigated by comparing the relationship between response and trial histories. Various terms are used in the literature to describe the bias, including sequential dependencies (Treisman & Williams, 1984), primacy and recency effect (Byrne, Lamberth, Palmer, & London, 1969), and more recently, serial dependence (J. Fischer & Whitney, 2014).

Definitions for serial effects differ depending on how they were tested. For instance, memory studies describe serial effects as the tendency of recalling recent items and the initial item after a duration has lapsed following learning (Deese & Kaufman, 1957; Murdock Jr, 1962). In psychophysical experiments, serial effects can be attractive and/or repulsive. In 1.0.1 and 1.0.2, we describe and present a list of non-exhaustive evidence for each type of serial effects.

1.0.1.1: Attractive serial effects

Gibson (1929) called serial effects “*assimilation*” because he showed that later responses always looked like the initial response. In his experiment, participants reproduced figures several times after viewing them once. Subsequent drawings often looked like the first drawing even if participants did not intentionally mimic their drawings. Evidence of attraction, in which the current response is more alike the preceding response, is observed in judging pitch (Alais, Orchard-Mills, & Van der Burg, 2015; Arzounian, de Kerangal, & de Cheveigné, 2017), loudness (Holland & Lockhead, 1968; Jesteadt, Luce, & Green, 1977), or cross-modally between visual area and loudness (Green, Luce, & Duncan, 1977). Thus, serial effects can be attractive by assimilating the current response to the previous response.

1.0.1.2: Repulsive serial effects

Serial effects are repulsive when responses to the current stimulus are repelled away (i.e. opposite) from the preceding response. For example, observers were recruited in an experiment to judge groups of light, medium, and heavy weights (Turner, 1931). Each weight group consisted of a standard along with heavier and lighter weights. Whenever the standard was judged lighter than the previous weight, the subsequent weight would be judged heavier regardless of the group the weight belonged to. Evidence of repulsion, in which the current response is less alike the preceding response, is shown when comparing graphs (Jones, Weinrott, & Vaught, 1978), or statements (Byrne et al., 1969), or when reward durations differ (Campbell & Wells, 1970). In summary, serial effects in psychophysical experiments can be attractive or repulsive.

Many effects observed in psychophysical experiments resemble serial effects. However, upon closer inspection, one eventually arrives at the conclusion that they are

indeed not serial effects. In the next few sections, we present two common effects and evaluate how they do not fit the criteria for serial effects.

1.0.2: Adaptation is not serial effect

The first type is called adaptation. Adaptation begins at the neuronal level. Neurons are limited by their ability to generate signals under prolonged stimulation. Overstimulation causes fatigue. Neurons prevent fatigue by changing their firing profile to the constant stimulation (Carandini, 2000). Once adapted, the neuron adopts a different membrane potential and firing rate to the same stimulation. A new stimulus with *similar* attributes as the previously adapted stimulus does not draw large responses. Instead, a stimulus with *different* attributes as the adapted stimulus elicits greater responses (Helson, 1964a, 1964b; Helson & Nash, 1960).

Adaptation causes *aftereffects*. Aftereffects are transient opposites from the adapted information when stimulation ceases. For instance, after adapting to a clockwise rotating wheel, the momentary aftereffect causes a stationary wheel to “spin” anti-clockwise (Anstis, Verstraten, & Mather, 1998). We observe aftereffects because the neurons are recovering from overstimulation (Clarke, 1961; Keck & Pentz, 1977). The aftereffects disappears once the neurons return to the original baseline firing rate.

1.0.2.1: Priming is not serial effect

Priming is the second type of effect observed in psychophysics which may resemble serial effect but is not. Priming is related to the experimental design. Priming experiments usually involve two phases: a learning phase and a test phase. Primes are only introduced in the learning phase. In the test phase, responses are biased by stimulus which share features with the prime. The consequence of priming is that responses become faster and sometimes more accurate (Biederman & Cooper, 1992;

Huang, Holcombe, & Pashler, 2004; Logan, 1990). Improved response speed and accuracy occurs even if observers were unaware of the prime (Dehaene et al., 1998), and can persist for a long time (Cave, 1997).

Priming may, on the surface, seem like a memorization strategy. However, priming is not memorization because no explicit/active recall is needed to associate the stimulus and the prime (Schacter, 1992; Tulving & Schacter, 1990). For instance, cortical activity decreases for primed objects, but increases during memory retrieval (Buckner & Koutstaal, 1998; Schacter & Badgaiyan, 2001). Patients with damaged explicit memory can also be primed (Shimamura, 1986; Tulving & Schacter, 1990).

1.0.2.2: Serial effects differ from adaptation and priming

Serial effects occur in psychophysical experiments. However, serial effects are different from adaptation and priming. Serial effects differ from adaptation because responses after adaptation are always opposite (i.e. repulsive) of the adaptor. Responses are assumed to be unbiased without adaptation. Serial effects do not require adaptation to bias responses. Serial effects occur due to the stimulus sequence, or the responses sequence. Previous stimulus/responses dictate whether current responses are attractive or repulsive.

Serial effects differ from priming. Serial effects do not require a learning phase since response biases are based on trial-to-trial changes. Priming experiments require a learning and a test phase to show priming. Responses are primed if the current stimulus is associated to the prime. Priming does not occur if there is no learning phase to establish the prime, or if the stimulus does not share similarities with the prime.

In summary, serial effects differ from adaptation and priming. Adaptation produces aftereffects which bias responses in the opposite direction of the adapted

information. Priming requires a learning phase and produces attractive responses only if the stimulus shares similar features as the prime. Serial effects happen due to the information over time: trial responses are biased by previous trials.

1.0.3: Revisiting if temporal stability is an expression of serial effects

According to temporal stability, perception is continuous when there are no differences between the previous and the current. This is because information is temporally stable over time. When we compare the previous information to current information, we experience serial effects and our response to the current information becomes biased. This suggests that temporal stability is a type of serial effect. The definition of temporal stability is like one type of serial effects called serial dependence. In the next few sections, we evaluate the literature to know more about serial dependence.

1.0.3.1: Serial dependence definition and how it works

Serial Dependence, proposed by J. Fischer and Whitney (2014), suggests that objects which are spatially similar and temporally closer together appear more alike than they are. This is observed objectively through participants' responses to the stimulus. Response errors in the current trial are biased by the relative differences between the stimulus from the previous and the current trial. Response errors to the current Gabor is more negative if the previous Gabor was more negative than the current Gabor. Similarly, response errors to the current Gabor is more positive if the previous Gabor was more positive than the current Gabor. This bias occurs when the previous and current Gabor differs by up to $\sim 10^\circ$ in orientation. J. Fischer and Whitney (2014) also showed that Gabors need not be presented at the same on-screen location for serial dependence. Serial dependence is present when attending to Gabors at different locations. For instance, large orientation differences ($\geq 45^\circ$) between the

previous and current Gabors do not elicit serial dependence, and there is no serial dependence for unattended Gabors. What mechanisms manifest serial dependence?

We visit some of them in 1.0.3.2–1.0.3.4.

1.0.3.2: Serial dependence in cell population processing

Serial dependence may represent low-level cell-population processing.

Neurons which are tuned to orientations communicate with neighboring neurons to create *continuity fields*. When a Gabor is first presented, the neuron best tuned to the Gabor orientation elicits the strongest activity. Neighboring neurons elicit weaker activity since they are less tuned to the orientation. When a new Gabor like the previous is presented, neurons firing from before gets heightened sensitivity to this new Gabor. The increased sensitivity biases perception towards the previous Gabor, showing serial dependence (J. Fischer & Whitney, 2014)

1.0.3.3: Serial dependence as working memory

Serial dependence may be associated with working memory during spatial judgments. Bliss, Sun, and D’Esposito (2017) manipulated the delay before the response phase and had participants remember the cue location while fixating. Participants then matched the cue location by moving a cursor. Results revealed increasing serial dependence for longer delays. The bias then decreased for delays beyond ten seconds. When Bliss and colleagues (2017) manipulated the ITI and kept the delay time constant, they showed that varying the ITI also varied serial dependence. Thus, they concluded that working memory played a role in this bias.

1.0.3.4: Serial dependence as responses to uncertainty

Serial dependence may be partially a response to uncertainty. Manassi, Liberman, Kosovicheva, Zhang, and Whitney (2018) partially replicated the experiment described in 1.0.10. However, they could not find serial dependence when

eliminating the response time delay. Instead, serial dependence was present when the stimulus contrast was drastically reduced. This increases the stimulus noise because the stimulus is now more difficult to discriminate. The authors concluded that while working memory plays a role in serial dependence, the uncertainty of the stimulus (i.e. noise) is equally important.

1.0.4: Serial dependence as an expression of temporal stability

From the literature, serial dependence spans from low-level cell population processing (1.0.3.2) to high-level representations of information such as working memory (1.0.3.3), and to more abstract information like uncertainty (1.0.3.4). The broad scope of serial dependence implies that this effect could possibly be an expression of temporal stability. That is, temporal stability uses serial dependence to evaluate previous and current information. If temporal stability is achieved simply by comparing information, then serial dependence is a viable candidate for investigating the limitations of temporal stability. Therefore, when we test serial dependence, we indirectly test temporal stability.

Using this argument, we can measure the type of information used for evaluating if the information was continuous. Continuity could be achieved either by integrating the previous and the current information, and the integrated information becomes continuous, or by discarding one of them and assigning the other as the continuous information. At this juncture, it remains unclear which information is integrated or discarded by serial dependence. In the following sections, we investigate serial dependence in various modalities and features to see what features of an information remains continuous.

1.0.4.1: Serial dependence is evident in vision studies but limited in audition

Our current understanding of serial dependence is mainly based on visual experiments. This is because serial dependence is predominantly shown by testing visual stimulus. These includes discrimination of visual features like spatial frequency (Lages & Treisman, 1998), motion (Alais, Leung, & Van der Burg, 2017), and higher-level features like numerosity (Cicchini, Anobile, & Burr, 2014), facial expression (A. Liberman, Fischer, & Whitney, 2014; A. Liberman, Manassi, & Whitney, 2018) and attractiveness (Taubert, Van der Burg, & Alais, 2016).

Evidence for serial dependence in audition is limited (Alais et al., 2015; Jesteadt et al., 1977). For instance, Alais et al. (2015) presented 100 ms gliding tones and participants had to judge if the tone glided upwards or downwards. Alais and colleagues found that the glide direction from previous trials could bias the responses in subsequent trials. What other auditory features also exhibit serial dependence?

1.1.0: Experiment 1.1 investigates serial dependence for pitch

We do not know what other auditory features show serial dependence. Thus, the purpose of the experiment was to test whether serial dependence was observed in other auditory features. We investigated serial dependence in pitch judgements (Experiment 1.1). We adopted the serial dependence paradigm by using a method-of-adjustment task instead of a 2-alternative forced choice task. We hypothesized that there is serial dependence in pitch if the current responses were attracted toward the previous stimulus.

Methods**1.1.1: Participants are musicians**

We recruited 13 participants ($M = 23.85$ years old, $SD = 4.24$, 7 females) from a music program for the experiment. This number was based on the original serial

dependence study (J. Fischer & Whitney, 2014). On average, participants practiced music for 11.42 years ($SD = 4.85$). The task was to respond to the stimulus by selecting the correct pitch an octave (half of the current frequency) below the stimulus. We previously recruited non-musically trained participants, but they could not complete the task accurately. Each participant completed 416 trials and was awarded S\$10/hr or course credits. The experiment was approved by Nanyang Technological University's institutional review board (IRB).

1.1.2: Apparatus

The experiment was programmed using MATLAB R2015a with Psychtoolbox 3 (Brainard, 1997; Kleiner et al., 2007). A pair of over-ear Creative Aruvana Live! Headphones (frequency response = 10 Hz – 30 kHz) was used for the experiment. Sinusoids were generated during the experiment at a sample rate of 44.1 kHz and presented binaurally. The fixation dot was presented on a 20" Sun Microsystems CRT monitor at a resolution of 1152 x 864 (100 Hz). A chin rest was positioned 57 cm away from the monitor.

1.1.2.1: Stimulus are two sets of pitch an octave below the other

A white fixation dot (diameter = 0.5°) was shown at the center of a black screen (white = 132 cd/m^2 , black = 0.75 cd/m^2). The stimulus tones were sinusoids between 500–999 Hz. The response tones were an octave below, between 250–499.5 Hz. In our pilot experiment, the task became trivialized if the stimulus and response tones shared the same frequencies. Figure 1.1.1 illustrates the stimulus and sequence of the experiment.

Figure 1.1.1 Trial sequence for Experiment 1.1. A 0.5° fixation dot appeared on the screen. Participants did not need to fixate since the experiment was entirely auditory. On each trial, participants heard a random pitch. The 500 ms stimulus was followed by a 1000 ms burst of white noise. The inter-stimulus interval (ISI) was 250 ms. During the response phase, participants moved the computer mouse left/right to match the response tone (i.e. a pitch) to the stimulus tone. The on-screen cursor was hidden. Participants heard the response tones continuously. Response tones morphed in real time based on the horizontal mouse coordinates. Clicking the computer mouse finalized the response and ended the trial. There was no time limit to respond. The inter-trial interval (ITI) was 2000.

The justification of using an octave difference between the tones was based on past studies (A. Smith, May, & Lyman, 1983). We did not use other ranges for the response tones because the task would be too difficult as the observer would have to perform some mental computation to match the tones. White noise was generated to mask the stimulus.

1.1.3: Procedure

Participants provided consent, wore headphones, and sat in a quiet room. Instructions appeared on the monitor. The instruction was to match the response tones to the stimulus tones. The experiment started after participants clicked the computer mouse. On every trial, participants heard a random stimulus for 500 ms, followed by a

1000 ms burst of white noise, then a 250 ms inter-stimulus interval (ISI), before the response phase.

At the response phase, the initial response pitch was randomized. Participants heard the response pitch continuously. The pitch changes when participants moved the mouse left/right (i.e. pitch decreases when the mouse moves leftward). Participants matched the response tone to an octave below the stimulus. We hid the on-screen cursor so that participants could not use it as response cues. The mouse click confirmed the response and ended the trial. A 2000 ms inter-trial interval (ITI) followed immediately.

There was no requirement to fixate since the experiment was completely auditory. Participants practiced for 20 practice trials (discarded from the analysis) before the experiment began. They were also instructed not to hum the pitch during the experiment or use other external aids to help them with the task. Participants completed 4 blocks of 104 trials in total. Each block lasted approximately 10 minutes.

1.1.4: Analysis and general descriptions

The analysis was conducted in MATLAB using basic computations and the curve fitting toolbox (Mathworks Inc., Nattick, MA, USA). We investigated serial dependence by evaluating response errors across trial histories (J. Fischer & Whitney, 2014). Subtracting response from stimulus produced response errors. Positive errors indicated that participants responded with higher pitch than the stimulus. 1-back histories indicated the difference between current stimulus and the previous stimulus.

We quantified serial dependence by the direction (i.e. sign) between response errors and 1-back histories. The current trial response errors are positive when the 1-back stimulus are positive. This indicates that the previous stimulus pulled the current trial responses toward the same direction.

1.1.4.1: Quantifying serial dependence by curve fitting

We calculated serial dependence by computing the average response errors across stimulus with a rolling window (bin width = 20°). We fitted the average response errors to a derivative of Gaussian (DoG) of the form $y = xawce^{-(wx)^2}$, where x is the distance between the n th stimulus and current stimulus, a is the amplitude of the function fit, w is the width of the curve, and c is the constant $\sqrt{2} \div e^{-0.5}$ (J. Fischer & Whitney, 2014). From the fit, the amplitude parameter, a , represented the magnitude of serial dependence. The constant c scales a so that positive values signified positive serial dependence (i.e. same direction).

1.1.4.2: Fixed effects analysis to measure serial dependence at the group level

Serial dependence can be a small and subtle effect at the individual level. Therefore, serial dependence at the group level is measured with fixed effects analysis (Fritsche, Mostert, & de Lange, 2017). This analysis involved pooling data across all participants to derive the group level response errors and the averaged response errors. We fitted the DoG curve to the group errors to calculate the amplitude of serial dependence.

1.1.4.3: Simulations

We did not conduct hypothesis testing because the data was contaminated by artifacts (see 1.2.6.1–1.2.6.3). This was confirmed by 1-back simulations to show that random responses in a linear stimulus space would produce results that imitated serial dependence. Simulated responses were derived from the stimulus histories of each participant. There were two sets of generated response errors following a Gaussian distribution: accurate ($M = 0$, $SD = 10$) and inaccurate ($M = 0$, $SD = 100$) errors. Each set was simulated 500 times. We then computed the average response errors of each set for every participant and visualized the results.

Results

1.1.5: Descriptive statistics and individual data

Participants were relatively slow at responding ($M = 4.51$ s, $SD = 1.89$).

Responses were accurate since the raw responses were scattered along the unity line (Figure 1.1.1). There were no obvious biases from the response plot. We visualized serial dependence by plotting average response errors against 1-back histories (Figure 1.1.2). Individual average response errors did not resemble serial dependence (Figure 1.1.3).

Figure 1.1.2 Plot of raw responses against stimulus in Experiment 1.1. Black line: unity line. Responses along the unity line are accurate responses (i.e. stimulus = response). Participants are generally accurate because the responses did not deviate far from the unity line.

Figure 1.1.3. Individual average response errors for Experiment 1.1. Gray: average response errors, red: data points. Response errors averaged using a 20° binning window.

1.1.5.1: Fixed effects analysis show no serial dependence and simulation found artifacts

We conducted fixed effects analysis to assess serial dependence at the group level (Figure 1.1.4a). The flat DoG indicated no serial dependence. There was no serial dependence in the data because of artifacts in the analysis.

Simulation was performed to show evidence of artifacts in the analysis. Accurate simulated errors did not exhibit serial dependence (Figure 1.1.4b). This was expected because veridical responses to the stimulus are bias-free. However, inaccurate simulated errors displayed some form of serial dependence (Figure 1.1.4c).

Hence, confidence testing was not conducted since testing would not produce meaningful results when the data was contaminated with artifacts.

Figure 1.1.4. a) Fixed effects analysis, b–c) simulated response errors. In a), gray: average response errors, blue: derivate of Gaussian (DoG) function. The DoG curve was flat and did not indicate any evidence of serial dependence. In b–c), responses were randomly sampled from a Gaussian distribution over 500 iterations for b) accurate errors ($M = 0$, $SD = 10$) and c) inaccurate errors ($M = 0$, $SD = 100$). Colors indicate the averaged response errors across all iterations for each simulated participant.

1.2.0: Experiment 1.2 investigates serial dependence for auditory locations

We tested for serial dependence in auditory localization. This experiment was identical to Experiment 1.1 except tones now conveyed spatial information (i.e. left-to-right). We hypothesized that there is serial dependence in auditory localization if the responses to the current spatial information were biased toward the previous spatial information.

Methods

1.2.1: Participants did not require musical expertise

Nine participants ($M = 23.11$ years old, $SD = 4.54$, 4 females) were recruited for the experiment. This number was based on the original serial dependence study (J. Fischer & Whitney, 2014). Participants did not require musical expertise. Participants had normal or corrected-to-normal visual acuity, no hearing problems, and gave consent prior to the start of the experiment. Each participant completed 416 trials and was awarded S\$10/hr or course credits. The experiment was approved by Nanyang Technological University's institutional review board (IRB).

1.2.2: Apparatus

The experiment was programmed using MATLAB R2015a (Mathworks Inc., Nattick, MA, USA), with Psychtoolbox 3 (Brainard, 1997; Kleiner et al., 2007). A pair of over-ear Creative Aruvana Live! Headphones (frequency response = 10 Hz – 30 kHz) was used for the experiment. Sinusoids were generated during the experiment at a sample rate of 44.1 kHz and presented binaurally. The fixation dot was presented on a 20" Sun Microsystems CRT monitor at a resolution of 1152 x 864 (100 Hz). A chin rest was positioned 57 cm away from the monitor.

1.2.2.1: Stimulus are tone locations using interaural differences

The auditory stimulus was a 3.2 kHz, 200 ms sinusoid. The response tone was a 1.6 kHz sinusoid to prevent adaptation to the stimulus. The response tone was heard continuously until a response was given. The available auditory *space* from our stereo headphones was 180°, where leftmost = -90°, straight ahead = 0°, and rightmost = 90°. The stimulus was presented within $\pm 60^\circ$ to discourage participants from selecting the extremes when responding. Responding to the extremes produced artifacts which hindered analysis (see 1.2.9 – 1.2.11). The response space was 180°. White noise was

presented immediately after the stimulus to mask aftereffects. The stimulus duration and trial sequence is illustrated in Figure 1.2.1.

Figure 1.2.1. Trial sequence for Experiment 1.2. A 0.5° fixation dot appeared on the screen. Participants did not need to fixate since the experiment was entirely auditory. Participants heard a random position for 200 ms every trial followed by 400 ms white noise. The inter-stimulus interval (ISI) was 250 ms. During the response phase, participants moved the computer mouse left/right to match the response tone location to the stimulus tone location. The on-screen cursor was hidden. Participants heard the response tones continuously. Response tones morphed in real time based on the horizontal mouse coordinates. Clicking the computer mouse finalized the response and ended the trial. There was no time limit to respond. The inter-trial interval (ITI) was 1000 ms.

We positioned the tones in using interaural level differences (McFadden & Pasanen, 1976; Middlebrooks & Green, 1991; Wightman & Kistler, 1992) by creating a logarithmic scale based on Fechner's Law to calculate 100 increasing loudness values beginning from zero (Fechner, 1860; Stevens, 1961). Both headphone channels received loudness ratio assignments between 0 – 100: leftmost = 100:0, straight ahead = 50:50, and rightmost 0:100. Approximating loudness with the logarithmic scale is the simplest method, although inaccurate (Stevens, 1961, 1966).

1.2.3: Procedure

Participants matched the response tone position to the stimulus tone position. On every trial, the stimulus appeared at a random position before the noise mask and ISI. Participants heard a random initial response tone position continuously until they moved the mouse left/right. This caused the response tone to move according to the horizontal cursor position. The cursor was hidden. Once participants made a response by clicking the mouse, the trial ended with a 1000 ms ITI. Participants completed 40 practice trials before commencing with the experiment. Participants completed 4 blocks of 104 trials in total. Each block lasted approximately six minutes.

1.2.4: Identical analysis to experiment 1.1

The analysis was identical to Experiment 1.1 (1.1.4-1.1.4.3). Briefly, the analysis was conducted in MATLAB using basic computations and the curve fitting toolbox (Mathworks Inc., Nattick, MA, USA). We calculated response errors by subtracting responses from the stimulus. Positive errors indicated that participants responded more rightward than the stimulus. 1-back histories indicate the difference between current stimulus tone position and the previous stimulus tone position. We computed the average response errors across stimulus with a rolling window (bin width = 20°) and fitted them to a derivative of Gaussian (DoG) described in 1.1.4.1. From the fit, the amplitude parameter quantified the magnitude of serial dependence.

Fixed effect analysis was conducted to investigate serial dependence at the group level. Data across all participants was pooled to compute group level response errors and the group level averaged response errors. We fitted the DoG curve to the group errors to estimate the amplitude of serial dependence. Confidence testing for Experiment 1.2 was also not conducted due to artifact contamination (see 1.2.6.1–

1.2.6.3). We confirmed this by simulating 1-back data using the same parameters described in 1.1.7. Simulations exhibited produced results imitating serial dependence.

Results

1.2.5: Descriptive statistics and individual data

Participants, on average, responded quickly to the tone positions ($M = 2.63$ s, $SD = 1.23$). However, responses were inaccurate (Figure 1.2.2). Participants were biased toward the middle and the extremities. Individual plots suggested serial dependence due to the shape of the averaged errors (Figure 1.2.3).

Figure 1.2.2. Plot of raw responses against stimulus in Experiment 1.2.

Figure 1.2.3. Individual average response errors for Experiment 1.2.

1.2.5.1: Fixed effects analysis showed no serial dependence and simulations found artifacts

Fixed effects analysis did not show serial dependence because the fitted curve was flat (Figure 1.2.4a). This meant that there was no serial dependence amplitude estimated by the curve. This was further supported by simulations which illustrated artifacts that resembled serial dependence. Specifically, there was no serial dependence for accurate simulated responses (Figure 1.2.4b). However, simulated responses with inaccurate errors mimicked the empirical response errors. This meant that the errors observed in the individual plots (Figure 1.2.3) and at the group level (Figure 1.2.4a) were due to artifacts (Figure 1.2.4c).

Figure 1.2.4. a) Fixed effects analysis, b–c) simulated response errors in. In b–c), responses were randomly sampled from a Gaussian distribution over 500 iterations for b) accurate errors ($M = 0$, $SD = 10$) and c) inaccurate errors ($M = 0$, $SD = 100$). Colors indicate the averaged response errors across all iterations for each participant.

Discussion

1.2.6: Inconclusive results for experiment 1.1 and 1.2 due to artifacts

Only a handful of studies showed auditory serial dependence. We investigated if pitch (Experiment 1.1) and auditory locations (Experiment 1.2) were subjected to serial dependence. Participants with musical expertise participated in Experiment 1.1 but we found no serial dependence for pitch. A separate group of participants completed Experiment 1.2, and again, we found no serial dependence for localization.

In both experiments, individual response errors appeared to have a serial dependence trend. However, the simulated response errors matched those from the individual data. This demonstrated the presence of artifacts in linear stimulus space.

We also found another response bias in Experiment 1.2. Participants favored responding to the extremities and straight-ahead. From our results, we concluded that Experiments 1.1 and 1.2. did not provide compelling evidence for serial dependence in pitch and auditory location.

1.2.6.1: Edge artifacts from a linear stimulus space confounded serial dependence analysis

Both experiments used a linear stimulus space (i.e. low-to-high frequency, left-to-right positions) which produced artifacts during analysis. This was demonstrated in our simulations (Figure 1.1.4c and 1.2.4c). Artifacts are seen near extreme values (smallest/biggest). For example, let us assume the stimulus history between two stimulus (previous – current: $-60^\circ - 30^\circ$) is -90° . Response errors to the current 30° stimulus may be 0° , positive, or negative. Positive or negative response errors fall along the ends of stimulus history; the horizontal axis (Figure 1.2.5).

Figure 1.2.5. Artifact during serial dependence analysis for 1 participant. The averages resembled serial dependence. However, it is an artifact from the response space.

The tendency the respond straight-ahead creates another problem. When participants responded straight ahead (0°) the response error for the current trial becomes $0^\circ - 30^\circ = -30^\circ$. Errors accumulate at the ends of the horizontal axis and is problematic for analyzing serial dependence. When the average response error is

calculated with the rolling window, which begins from one end of the axis, errors at the ends of the axis causes the average to look like serial dependence.

1.2.6.2: Edge artifacts do not disappear by omitting data from extremities

Edge artifacts that imitate serial dependence do not disappear simply by omitting data from the extremities. Serial dependence fit did not improve when omitting data from the extremities on the x- and y-axis for Experiment 1.1 (Figure 1.2.6) and Experiment 1.2 (Figure 1.2.7). Instead, group-level results from fixed effects analysis indicated minor changes to the average response errors. This was expected since there were fewer data used to compute the average.

Figure 1.2.6. Data progressively omitted from the extremities for Experiment 1.1 did not improve serial dependence fit. Response errors from the extremities along the x-axis, y-axis, and both x- and y-axis were removed to investigate if serial dependence fit could be improved. The serial dependence fit remained flat across all analysis.

Figure 1.2.7. Data progressively omitted from the extremities for Experiment 1.2 did not improve serial dependence fit. The serial dependence fit remained flat across all analysis.

1.2.6.3: Linear stimulus space causes artifacts

Both experiments used a linear stimulus space (i.e. low-to-high frequency, left-to-right positions) which produced artifacts during analysis. These artifacts could not be explained mainly by the participants because our simulated results also exhibited the artifacts. There were no artifacts when the simulated responses were accurate (Figure 1.1.4b and 1.2.4b). Artifacts were recreated when the simulated responses were error prone (Figure 1.1.1.4c and 1.1.2.4c). Therefore, we concluded that the linear stimulus space caused the results to look like serial dependence.

This problem with artifacts in linear spaces is eliminated by adopting a circular response space. Data is wrapped to the opposite direction (see J. Fischer and Whitney, 2014, and Liberman et al., 2014). In linear space, the data cannot be converted into the opposite direction because the opposite direction does not exist (e.g. previous – current: $-60^\circ - 30^\circ$ is unlike previous – current: $30^\circ - 60^\circ$). In a circular space, half

the circle (181° – 360°) is redundant information. When we remap 0° – 180° to $\pm 90^\circ$, 1° and 181° becomes remapped to -89° because they are redundant. Similarly, -60° (210°) is represented by 30° . In Experiment 1.3, we mapped a stimulus onto itself to create a circular space (see 1.3.2.1).

1.2.6.4: Central tendency bias when responding to auditory positions

In this section, we discuss possible reasons for other forms of response biases. Participants in Experiment 1.2 frequently responded to the straight-ahead and extreme positions. The tendency to respond straight-ahead could be explained by the central tendency bias (Hollingworth, 1910). The bias occurs because the observer creates an average estimate of all the stimulus. In Experiment 1.2, the average spatial location across the $\pm 90^\circ$ response space was 0° . This location corresponded to the straight-ahead position. Our data suggested that participants could have exhibited central tendency biases, since responses aggregated around the straight-ahead position (Figure 1.2.1).

The central tendency bias could be exacerbated because participants could not tell where the sounds were coming from. In the real world, we hear sounds from outside the head. Sounds through the headphones are perceived *inside* the head (Plenge, 1974). Audio presented over headphones do not carry all available spatial signals as compared to the natural world. In natural hearing, our brain computes the distance of a sound based on a head-related transfer function (Mehrgardt & Mellert, 1977). This is the value for sound direction and pressure differences between the outer ear and the inner ear. Natural listening is simulated through headphones when the head-related transfer function is added to the audio. The head-related transfer function, unique to the listener, allows the listener to identify the horizontal position of the sound accurately as if the sound came from outside the headphones (Wightman &

Kistler, 1989). Since our stimulus did not contain head-related transfer function, participants faced difficulties deciding sound locations because the sounds appeared inside the head. Thus, participants likely resorted to straight-ahead reports.

1.2.6.5: Criticisms of current methods to determine auditory locations

Auditory locations were computed using interaural-level differences. Assigning locations via this method may not adequately partition auditory spaces in equally. As a result, locations at the extremities become fuzzy and difficult to discriminate. Locations which are fuzzy become ambiguous. When observers are tasked to discriminate ambiguous locations, they likely use the louder sound to estimate the ambiguous positions. This is because the louder sound dominates and eliminates the weaker sound if the two sounds differ by 12 dB. Such observations are evident when the overall loudness across the two sounds do not exceed 40 dB (Deatherage & Hirsh, 1959), which is equivalent to the sound of a computer that was switched on (Chepesiuk, 2005).

Loudness was not measured in our experiment. Participants could adjust the loudness at the start of the experiment if the sound were too soft/loud. This does not discount the fact that participants in Experiment 1.2 could have responded to the louder sound on one side of the headphones. This could explain why we found responses at extremities even when the stimulus was never presented at those positions. This issue is circumvented by hearing the softer sound first (Sayers, 1964). However, hearing the softer sound before the louder sound distorts the auditory position.

1.2.6.6: Fixation and lateralization effects

Auditory lateralization is biased by gaze position. Observers tend to perceive sound coming from the location they are looking at, even if the current environment is

in complete darkness (Lewald & Ehrenstein, 1996). In Experiment 1.2, participants did not have to fixate. Participants could move their eyes freely during the experiment. Participants could have responded to the extremities if they looked away from the monitor. Since there was no fixation spot, we could not ascertain if participants were responding accurately to the stimulus or if their responses were biased by their gaze position.

1.2.7: Semantic information and the concept of circular space

Verbal and non-verbal sounds convey semantic and acoustic information (Eustache et al., 1995; Tillmann, Schulze, & Foxton, 2009). Semantic information enables language comprehension through words or symbols to convey meaning (Demonet et al., 1992; Gainotti & Lemmo, 1976; Koelsch et al., 2004). Acoustic information allows the listener to detect changes in sound such as pitch variations and modulations (Foxton et al., 2003; Hall et al., 2002; Warrier et al., 2009), or fluctuations in harmonic structures (Omori, Kojima, Kakani, Slavits, & Blaugrund, 1997; Rauschecker & Scott, 2009). Non-verbal acoustical information from the previous experiments did not produce good evidence for serial dependence. Therefore, in the following experiment, we tested if verbal information (semantics) could better elicit serial dependence.

Speech sounds are a combination of phonemes and phonetic units. Phonemes are individual perceptual blocks of sounds in a word (Twaddell, 1935). Vowels are part of phonemes which enables comprehension. In the English language, alterations to a vowel can cause an observer to mishear the spoken word (Hogan & Rozsypal, 1980; Van Ooijen, 1996). However, it is important to note that vowel discrimination is strongly influenced by phonetic experience. An observer is more sensitive to phonemes associated with their language experiences as compared to phonemes in

other languages (Miyawaki et al., 1975). To minimize this influence on vowel discrimination, one can recruit native speakers or bilingual speakers who are exposed to the vowels early in life (Flege, MacKay, & Meador, 1999). Commonly identified English vowels include /ɜ:/, /u:/, and /ɑ:/ (Hillenbrand, Getty, Clark, & Wheeler, 1995). Therefore, the following experiment uses these three vowels to investigate if there is serial dependence in semantic information.

In the previous experiments, there were artifacts produced by linear stimulus space. This hindered the analysis because a simulated effect could imitate the shape of serial dependence. It was difficult to know if there were real effects from the experiments. The solution to eliminate such artifacts is to adopt a circular stimulus space. A. Liberman et al. (2014) demonstrated the solution by morphing three distinct stimuli. Each stimulus was morphed over several morph steps onto another stimulus to create a circular response space. An auditory circular space can be created using this concept. Each vowel morphs over several steps onto another vowel. The vowels /ɜ:/, /u:/, and /ɑ:/ would be morphed like so: /ɜ:/ ↔ /u:/ ↔ /ɑ:/ ↔ /ɜ:/, to achieve a circular auditory space.

1.3.0: Experiment 1.3 investigates auditory serial dependence in vowels

The purpose of Experiment 1.3 was to test if there was serial dependence in semantic information. We created a circular response space by morphing three vowels: /ɜ:/, /u:/, and /ɑ:/. Data analysis for serial dependence was identical to those described in Experiment 1.1 and 1.2. We evaluated if response errors for the current trial were influenced by the previous stimulus. We hypothesized that serial dependence was depicted in verbal information if responses to the current vowel were influenced by the previous vowel.

Methods

1.3.1: Participants

The number of participants recruited was adapted from the original study (J. Fischer & Whitney, 2014). 12 participants ($M = 26.92$ years old, $SD = 6.20$, 5 females) took part in Experiment 1.3. Participants had normal or corrected-to-normal visual acuity, no hearing problems, and gave consent before the experiment. They were awarded S\$10/hr or course credits after the experiment. The experiment was approved by Nanyang Technological University's institutional review board (IRB).

1.3.2: Apparatus

The experiment was programmed using MATLAB R2015a (Mathworks Inc., Natick, MA, USA), with Psychtoolbox 3 (Brainard, 1997; Kleiner et al., 2007). Participants heard the auditory stimulus using a pair of over-ear Creative Aruvana Live! Headphones (frequency response = 10 Hz – 30 kHz). A chin rest was positioned 57 cm away from a 20" Sun Microsystems CRT monitor at a resolution of 1152 x 864 (100 Hz).

1.3.2.1: Stimulus

The experiment utilized synthesized vowels from the MATLAB audio toolkit (S. Smith, 2011). This toolkit contains a *vowel* function which produces distinguishable synthesized vowels following parameters described in Peterson and Barney (1952). Synthesized vowels were morphed along a circular continuum with the vowel sounds /ɜ:/, /u:/, and /ɑ:/ as anchors (Figure 1.3.1a). A pilot study confirmed that participants could distinguish the vowels.

Synthesized vowels occupied a circular continuum of 360° space. However, serial dependence literature examines only half the circle because the other half is remapped onto first half at $\pm 90^\circ$ (J. Fischer & Whitney, 2014). This was because a

Gabor, rotated by 180° , appears as if it was at 0° . Therefore, our auditory circle was converted into 180° space to be consistent with the literature. From this conversion, the /ɜ:/ vowel mapped onto itself at $0^\circ/180^\circ$ (Figure 1.3.1a).

Figure 1.3.1. Vowel continuum and trial sequence. **(a)** The vowels, /u:/, /ɜ:/, and /ɑ:/, were morphed along a circular continuum. There were 100 morph steps between each vowel pairs. **(b)** Sequence of a single trial in Experiment 3. Participants heard a 500 ms stimulus vowel, then a 1000 ms auditory noise. The inter-stimulus interval (ISI) was 250 ms. During the response phase, participants heard the response vowels continuously. The task was to match the response vowels to the stimulus vowels on the same trial by moving a computer mouse. The trial ended when participants clicked the computer mouse to indicate their response. The inter-trial interval (ITI) was 2000 ms.

1.3.2.2: Vowel synthesis and auditory noise

We now describe the vowel synthesis procedure. Figure 1.3.2 illustrated the formant frequencies (F1, F2, and F3) for the synthesized vowels in the experiment. Synthesized vowels had a fundamental frequency (F0) of 122 Hz, sampling rate = 44.1 kHz. This corresponded to a male vowel (see Table II in G. E. Peterson & Barney, 1952). This F0 was held constant for all vowels synthesized. Thus, vowels did not vary in terms of pitch. The synthesis script from the toolkit then created a stream of glottal pulses using the F0 and the sampling rate. For each vowel, the script used a

triangular approximation to ensure that the amplitude of the synthesized vowel was kept constant.

Figure 1.3.2. Formant frequencies of each vowels. Each line indicates the first (red), second (blue), or third (black) formant frequency.

The synthesis script passed each formant frequency through a 1-dimension rational transfer function filter (Oppenheim, 1999). This filter modelled formants in speech signals. The script kept the formant bandwidth constant at 50 Hz. After that, an impulse train was filtered by two first-order filters at 250 Hz to simulate tract transfer function. The tract transfer function simulates actual vowel tract vibrations (e.g. see Akande & Murphy, 2005). The filtered impulse train and each of the filtered formant frequencies were combined in a tapered-cosine window to create the synthesized vowel.

We created equidistant increments of formant frequencies between vowel pairs. There were 100 linear increments (steps) between each vowel pair, totaling 300 steps across the three vowels. This produced a continuum of 300 sets of linearly

spaced formant frequencies (/ɜ:/ ↔ /u:/ ↔ /ɑ:/ ↔ /ɜ:/). Each set of formant frequencies produced a single vowel from the synthesis script. This process, repeated 300 times, produces the auditory circular space of morphed vowels. From here on, we employ the terms *stimulus* vowel and *response* vowel to denote the vowels heard at the start of the trial and during the response phase, respectively.

Temporal scrambling is a process in which the auditory spectra of a sound is reshuffled (Ellis, 2010). We generated auditory noise by temporally scrambling the morphed continuum derived from the three canonical vowels. This was to mask auditory aftereffects. Temporal scrambling preserved the feature space of the auditory stimuli without making it intelligible: The noise sounded *like* the vowels without containing information about any one vowel. Scrambled masks are effective at masking the stimulus information (Brungart, 2001). We faded-in and out to the first and final millisecond of the auditory stimuli to eliminate clicking artifacts.

1.3.3: Procedure

The procedure of the experiment was as follows (Figure 1.3.1b): on each trial, participants heard a random 500 ms vowel morph and a 1000 ms scrambled noise. There was an ISI of 250 ms before the response phase. During the response phase, participants matched the response vowels to the stimulus vowel by moving a computer mouse left/right. Response vowels were morphed in real time to the horizontal coordinate of the mouse cursor. The cursor was hidden from the screen.

Participants confirmed their responses by clicking the computer mouse. The initial response vowel morphed step was randomized every trial. The response vowel was heard continuously under a response was given. Participants completed four blocks of 104 trials in total. Each block lasted approximately 10 minutes. Participants also practiced for 30 trials before starting the experiment (excluded from analysis). We

instructed participants not to voice/utter the vowels or use external aids to help with the task.

1.3.4: Analysis for serial dependence

Serial dependence analysis was conducted in MATLAB using the curve fitting toolbox (Mathworks Inc., Nattick, MA, USA). We used the circStat toolbox to calculate angular statistics (Berens, 2009). The analysis was identical to the previous experiments. Briefly, response error was the difference between response and stimulus morph step. Errors beyond $\pm 90^\circ$ were remapped in the opposite direction. Positive errors meant that participants responded more *clockwise* to the stimuli (Figure 1.3.1a). Trials with response times beyond 20 seconds were discarded.

We conducted fixed effects analysis by pooling data across all participants to compute group-level response errors. Average response errors were calculated with a rolling window (bin width = 20°). The DoG function was fitted to the group response errors. We computed response errors up to 3-backs for individual and 5-backs for group-level data. We only presented individual data up to 3-backs since there were no similarities across individual data. This was also to reduce visual clutter.

1.3.4.1: Permutations for significance testing and confidence intervals

Significance testing was conducted by permutating the group data using the following procedure (B. Efron & Tibshirani, 1986): we shuffled the stimulus and raw response order without replacement, so that each response was still associated to the same stimulus. Data shuffling removed all forms of serial order effects by randomizing the stimulus histories. Therefore, permutations controlled for other potential artifacts that could induced a serial dependence-like bias, such as biases to respond to un-morphed vowels. Data shuffled over 10,000 iterations. In each iteration, we calculated group response errors, n-backs, and the DoG amplitude. We determined

the 95% confidence interval using the shuffled data amplitudes and compared the empirical amplitude to the permuted amplitudes. An empirical amplitude >95% of the shuffled amplitude was significantly different than chance ($p < .05$).

We calculated the bootstrapped standard error of means (SEM) and the 95% confidence intervals (C.I.) for all 5-back analyses using the permuted sample. Since hypothesis testing was based on bootstrapping, we calculated exact partial eta-squared (η_p^2) effect sizes for all 5-backs by comparing the empirical amplitude to the permuted amplitudes of the DoG curve. This analysis established the effect size of the empirical amplitude in relation to a randomly shuffled sample.

Results

1.3.5: Descriptive statistics

Participants were slow at judging vowels than in previous experiments ($M = 5.52$ s, $SD = 2.37$). There were three clusters from the raw responses (Figure 1.3.3). Each clusters centered about $0^\circ/180^\circ$, 60° , and 120° , corresponding to the three canonical vowels (see Figure 1.3.1a). This implied that participants were biased to respond to a canonical vowel than the actual morphed step. Individual average response errors for up to 3-backs did not resemble serial dependence (Figures 1.3.4–1.3.6).

Figure 1.3.3. Responses as a function of stimulus in Experiment 1.3. The boundaries outline the clusters corresponding to the three canonical vowels /ɜ:/, /u:/, and /ɑ:/. The cluster from the four corners correspond to the vowel /ɜ:/.

1.3.5.1: Individual response errors

There were large individual differences across participants based on qualitative assessments of the response errors (Figure 1.3.4–1.3.6). Response errors did not form any consistent patterns across participants. However, response errors within the participants were more regular. For instance, response errors for some participants were consistently higher than zero across all 3-back histories (e.g. AR, CW, and JV). However, this consistency was absent for other participants (e.g. AA, KC).

Figure 1.3.4. Experiment 1.3, individual average response errors, 1-back. Gray: average response errors.

Figure 1.3.5. Experiment 1.3, individual average response errors, 2-back.

Figure 1.3.6. Experiment 1.3, individual average response errors, 3-back.

1.3.5.2: Fixed effects analysis results

We conducted fixed effects analysis to investigate serial dependence at the group level (Figure 1.3.7). At the group level, the shape of the average errors reflected repulsive bias. The DoG closely matched the shape of the averages. Group responses hinted at a $.64^\circ$ serial dependence in 1-back. The fitted function was flat for 2-, 3-, and 4-back histories. The amplitudes for the flat DoG was $.002^\circ$ for 2-back, $.74^\circ$ for 3-back, and $.005^\circ$ for 4-back histories. There was a repulsive effect of $.56^\circ$ for 5-back histories. Permutation analysis did not indicate any statistically significant effects in 1-back ($p = .41$), 2-back ($p = .99$), 3-back ($p = .34$), 4-back ($p = .99$) and 5-back ($p = .50$) histories. Table 1.3.1 shows the bootstrapped error estimates, confidence intervals, and effect sizes for Experiment 1.3.

Figure 1.3.7. Fixed effects analysis, Experiment 1.3. a–c) N-back histories up to 5-backs, gray: average response errors, blue: fitted derivative-of-Gaussian (DoG) curve. Peak amplitudes from the DoG were a) 0.95° , b) 1.07° , c) 1.03° , d) 0.81° , e) 0.67° , and indicated repulsive effects. The fitted DoG closely matched the shape of the averages.

Table 1.3.1 Experiment 1.3 bootstrapped error estimates, confidence intervals, and effect sizes

N-back	Auditory (A)	
	Error estimates	η_p^2
1-back	$.64^\circ \pm .08^\circ (-2.18^\circ - 1.76^\circ)$	.23
2-back	$.002^\circ \pm .07^\circ (-2.13^\circ - 1.77^\circ)$	.003
3-back	$.74^\circ \pm .08^\circ (-2.14^\circ - 1.81^\circ)$	.28
4-back	$.005^\circ \pm .07^\circ (-2.16^\circ - 1.78^\circ)$	.002
5-back	$.56^\circ \pm .07^\circ (-2.16^\circ - 1.81^\circ)$	.12

Discussion

1.3.6: Experiment 1.3 did not find serial dependence in vowels

Sounds convey verbal (semantics) and non-verbal information in the natural world. Previous experiments using non-verbal sounds (i.e. pitch and location) did not produce convincing evidence for serial dependence. In this experiment, we investigated whether vowels would elicit greater serial dependence. Vowels were

morphed to create a circular space to avoid edge artifacts in the analysis. We found that participants frequently responded to the canonical vowels instead of the ambiguous vowel morphs. Our results did not exhibit serial dependence.

1.3.6.1: Vowel boundaries, prototypes, and its role in vowel discrimination

The lack of serial dependence in the vowel stimulus could be because of vowel characteristics. Vowels have specific boundaries which dictate how good an observer identifies one vowel from the next. Auditory characteristics of a vowel can change within the boundary, but observers may not readily detect such changes. In contrast, observers readily identify vowel changes when the auditory characteristic changes to a different vowel boundary. The best discrimination between vowels only arises near the boundaries (Fry, Abramson, Eimas, & Liberman, 1962; A. M. Liberman, Harris, Hoffman, & Griffith, 1957).

Vowel categories create prototypes and these prototypes form within categorical boundaries. Prototypes are perceptual long-term memory units which readily match a stimulus that fall within the boundary (Repp, 1977). Prototypes work the following way in speech perception; feature identification is based on a fuzzy-logic model where speech features are first evaluated before undergoing prototype matching (Oden & Massaro, 1978). During feature evaluation, continuous acoustic features are assigned varying weights. The varying degree of the weights makes feature identification fuzzy as compared to discrete weight assignments. Each set of varying weights then undergoes prototype matching in the long-term memory. Sets of matched prototypes are classified probabilistically to identify the speech percept.

Vowel discrimination is affected by prototypes. Different vowel boundaries create a perceptual effect in humans called the *perceptual magnet effect* (Kuhl, 1991). This effect describes the relationship between prototypes and sounds within a vowel

boundary. The prototype acts like a magnet, attracting the perception of other sounds within the boundary. Therefore, observers readily attribute sounds within the vowel boundary to the prototype in comparison to sounds in other vowel boundaries. However, prototypes may not necessarily influence vowel discrimination. For example, Schwartz, Abry, Boë, Ménard, and Vallée (2005) argued that successful discrimination of vowels is due to the distinctness of vowels, rather than the prototypicality of them. They showed, using different formant frequencies, that vowels sharing similar formants are attractive and serve as references for vowel discrimination. Therefore, new vowels with different formants are readily perceived as different.

Vowel prototypes influence the discrimination of current vowels. It remains valid to argue that categorical perception of vowels and vowel prototypes could explain for the lack of serial dependence in vowels. Therefore, one may justify why vowels were an inappropriate stimulus for serial dependence. However, is there no serial dependence because of categorical stimulus/perception?

1.3.6.2: Serial dependence is evident in categorical face perception

It is not a well-justified argument to say that categorical stimuli are inappropriate in a serial dependence experiment. Serial dependence exists for categorical perception. One example is face perception. Face perception is categorical (Freeman, Rule, Adams, & Ambady, 2009). It also demonstrates boundary effects like those in vowel perception because ambiguous faces belonging to a boundary are often identified as the face represented by that boundary (Beale & Keil, 1995). While unfamiliar faces may not be readily associated to categories, learning creates categories for these unfamiliar faces. For instance, whether an ambiguous face is male or female soon gets classified into male/female categories after observers learn the

faces (Bülthoff & Newell, 2004). This learning process happens without prior experience. Children with early-onset blindness, but regained sight through surgery in later life, learn to categorize faces (T. K. Gandhi, Singh, Swami, Ganesh, & Sinha, 2017). Individual emotions expressed from within each face are also categorized. Emotions in the opposite spectrum (i.e. happy vs sad), are readily recognized and identified (Etcoff & Magee, 1992).

Categorical face stimuli show serial dependence. A. Liberman et al. (2014) demonstrated this evidence when participants judged the face identity of morphed faces in a continuum. There was also serial dependence when faces were viewed in profile. Another categorical feature of face perception is attractiveness. Children learn from a very early stage how to categorize facial attractiveness (Ramsey, Langlois, Hoss, Rubenstein, & Griffin, 2004). Facial attractiveness is also susceptible to serial dependence (Xia, Leib, & Whitney, 2016). These studies show that categorical stimuli are affected by serial dependence. Therefore, arguing that vowels were inappropriate stimuli because they are categorical is not well justified. Categorical perception remains subjected to serial dependence.

1.3.6.3: Awkward vowel morph steps

The lack of serial dependence in Experiment 1.3 could be due to the awkward morph steps between vowels. Each vowel was morphed onto another in 100 steps. This produced a total of 300 individual auditory stimuli. However, the auditory response space was then compressed into 180°, to mimic Gabor orientations. This compression might have influenced the serial dependence analysis. There was no prior reasoning why one vowel was morphed onto another in 100 steps. Since the goal of morphing vowels was to create a circular space, and the space was to be identical to a

Gabor, then morphing one vowel to the next over 60 steps would better mimic Gabor orientations. This was implemented in the following experiment.

1.4.0: Is serial dependence perceptual or decision?

Parts of the following experiments were previously published (Lau & Maus, 2019b). The lack of serial dependence in audition may indicate that the effect only affects vision. However, before we arrive at this conclusion, there is a recent debate on whether serial dependence occurs at the perceptual level or at the decision level.

Fritsche et al. (2017) presented evidence which suggests that serial dependence was related to post-perceptual decisions. In their experiment, participants had to sustain the Gabor orientation information in working memory for either 300 ms or 3750 ms before reproducing the orientation during response. There was positive serial dependence bias for the longer delay. Additionally, participants who experienced the greatest serial dependence bias also experienced the largest repulsion when responding with a 2-alternative forced-choice paradigm instead of a method-of-adjustment task. These results implied that the type of decision made during a trial affects whether positive or negative serial dependence was observed and led the authors to attribute serial dependence to post-perceptual decision processes rather than perception itself. Similarly, Pascucci et al. (2019) suggested a multi-stage model that combines perceptual aftereffects and attractive decision biases to explain serial dependence effects.

Other researchers argue that serial dependence is a perceptual effect. For example, Cicchini, Mikellidou, and Burr (2017) first replicated the results of Fritsche et al. (2017) by showing that negative effects (i.e., repulsion) occurred when successive stimuli were largely different ($> 20^\circ$). They further analyzed the response errors for stimuli with smaller differences ($< 10^\circ$) and found positive serial

dependence. In a separate experiment, Cicchini et al. (2017) provided more support for perceptual origins of serial dependence by showing that when successive stimuli were similar, there was strong serial dependence even when participants had to respond with an orthogonal orientation. When successive responses were similar and successive stimuli were orthogonal, there was no serial dependence. Further, serial dependence was shown to be tuned to specific stimulus locations (J. Fischer & Whitney, 2014), which seems in contrast with a high-level decision account.

Participants demonstrate serial dependence bias even when recall memory for the previous stimulus is poor (J. Fischer & Whitney, 2014). Visually evoked potentials during passive viewing of random dot arrays were biased by the dot quantity from the previous trial (Fornaciai & Park, 2018). More recently, Fornaciai and Park (2019) showed that the numerosity of sequentially presented flashes can elicit attractive serial dependence when participants judge the numerosity of a subsequently presented dot array. They conclude that serial dependence is likely perceptual since this bias was observed for various visual presentation formats of numerosity, although the bias was absent when visual flashes were replaced with auditory tones.

1.4.0.1: Testing if serial dependence is perceptual or decision with a multimodal stimulus

The difficulty of evaluating if serial dependence is a perceptual or a decision effect could be restricted when using one modality. Serial dependence experiments commonly test single features. For example, participants always judged Gabor orientations (J. Fischer & Whitney, 2014; Fritsche et al., 2017) or faces (A. Liberman et al., 2014; A. Liberman et al., 2018). Participants in such tasks become accustomed to encoding the same stimulus feature and performing the same adjustment task

throughout the experiment. As such, participants expect to see and do the same thing on every trial.

Task expectations might contribute to serial effects. Expectation may facilitate visual processing by allowing us to more readily detect or recognize a stimulus (Summerfield & Egner, 2009). Participants in serial dependence experiments become accustomed to encoding the same stimulus feature and performing the same adjustment task throughout the experiment. Therefore, they expect to see and do the same thing on every trial. It is possible that this expectation influences how the current trial stimulus is discriminated, since even the encoding of the stimulus is done under the expectation to perform a subsequent decision on it. Evidence of serial dependence when such expectations on the task to be performed are eliminated would add compelling evidence to the recent perceptual/decision debate.

1.4.0.2: Experiments 1.4–1.6 test serial dependence using a multimodal stimulus

The following experiments were published in Lau and Maus (2019b). The goal of Experiments 1.4–1.6 was to determine the impact of task expectations on serial dependence. We presented a multimodal audio-visual stimulus on every trial and varied the task expectations across three experiments. In Experiment 1.4, we first tested serial dependence for the multimodal stimulus in the typical way. Participants were asked to ignore one modality and report the other modality repeatedly throughout the experiment. We found strong evidence for visual serial dependence, whereas our auditory stimulus and task did not elicit serial dependence.

In Experiment 1.5, we randomized the task on every trial to abolish strong task expectations. Participants had to pay attention to both modalities as they did not know which modality to report until the response phase. We again found serial dependence for reports on the visual modality, even when participants reported the auditory

modality on the previous trial and could not anticipate which modality was task relevant.

In Experiment 1.6, we further investigated expectation effects by additionally including no-response trials. Participants had to switch between reporting different modalities and, occasionally, making no responses. Again, the previous stimulus always influenced subsequent visual reports, but not auditory reports, regardless of whether a report was made in the previous trial.

Methods

1.4.1: Participants

Serial dependence is replicated for a wide number of participants (range: 7 – 24) in more recent studies (Cicchini et al., 2017; Fritsche et al., 2017). Thus, we recruited participants from this range. Participants ($N = 19$, $M = 23.74$ years old, $SD = 3.89$, 12 females) were recruited from undergraduate courses at Nanyang Technological University for Experiment 1.4. They were naïve to the purpose of the experiment, except for one. Eight participants ($M = 25.75$ years old, $SD = 4.71$) from Experiment 1.4 proceeded to complete Experiment 1.5.

Data from one participant for Experiment 1.5 was excluded for failing to complete both sessions ($N = 7$, $M = 26.0$ y/o, $SD = 5.03$). A new group of participants ($N = 10$, $M = 22.10$ y/o, $SD = 3.21$) were recruited for Experiment 1.6. Participants had normal or corrected-to-normal visual acuity, had no hearing problems, and gave consent prior to the start of the experiment. Upon completion, participants were either rewarded with course credits or up to S\$10/hr. The experiments were approved by Nanyang Technological University's Institutional Review Board.

1.4.2: Apparatus

The apparatus was the same as previous experiments. The experiment was programmed using MATLAB R2015a (Mathworks Inc., Nattick, MA, USA), with Psychtoolbox 3 (Brainard, 1997; Kleiner et al., 2007). Angular statistics were calculated using the circStat toolbox (Berens, 2009). A pair of over-ear Creative Aruvana Live! Headphones (frequency response: 10 Hz – 30 kHz) was used for both experiments. Visual stimuli were presented on a 20” Sun Microsystems CRT monitor at a resolution of 1152 x 864 and refresh rate of 100 Hz. A chin rest was positioned 57 cm away from the monitor.

1.4.2.1: Stimulus

A white fixation dot (diameter = 0.5°) was always shown at the center of a gray screen (gray = 64.19 cd/m², white = 132 cd/m², black = 0.75 cd/m²). The multimodal stimulus comprising of a Gabor patch and a vowel sound appeared for 500 ms. The Gabor orientation and the specific vowel were selected randomly. There was a systematic relationship between the Gabor and the vowel (Figure 1.4.1a). A 0° (vertical) Gabor corresponded to the /ɜ:/ vowel, a 60° Gabor corresponded to the /u:/ vowel, and a 120° Gabor corresponded to the /ɑ:/ vowel. Orientations in-between were related to in-between vowel morphs. For instance, a 15° Gabor was mapped to morph step 15 between the vowel /ɜ:/ and the vowel /u:/. We use *orientations*, *clockwise*, and *anti-clockwise*, to refer to both visual and auditory stimuli. Participants were initially naïve to the relationship, except for one.

Multimodal noise consisted of white noise pixels smoothed with a Gaussian kernel and a scrambled vowel morph continuum and was presented for 1000 ms immediately after the stimulus. Then, there was an inter-stimulus interval (ISI) of 250 ms before the response phase. There was no time-limit to make a report. After each

response, there was an inter-trial interval (ITI) of 2000 ms before the next trial (Figure 1.4.1b).

Figure 1.4.1. Gabor orientation, vowel continuum, and trial sequence. a) Examples of a Gabor presented at various orientations, and the Gabor relationship with the vowels, /3:/, /u:/, and /ɑ:/, morphed along a circular continuum. There were 60 morph steps between each vowel pair. b) Sequence of a single trial in all experiments. Participants fixated the dot and the multimodal stimulus (Gabor + vowel) was presented for 500 ms. Noise was presented for 1000 ms after the offset of the stimulus. There was an inter-stimulus interval (ISI) of 250 ms before the response phase. In Experiment 1.4, participants only saw the adjustment bar in condition V and only heard the response vowel in condition A. In Experiments 1.5 & 1.6, participants saw either the adjustment bar or heard the response vowel, prompting the appropriate response. Participants had to report to Gabor orientation if they saw the adjustment bar or report the stimulus vowels if they heard the response vowels. After a response was given by a mouse click, there was an inter-trial interval (ITI) of 2000 ms before the start of the next trial. In Experiment 1.6, 20% of the trials were no-response trials in which neither the adjustment bar nor the adjustment vowels were presented.

Parameters of the Gabor were adapted from J. Fischer and Whitney (2014).

Each Gabor was drawn with a fixed spatial frequency of 0.33 cycle/° at 25%

Michelson contrast, using a Gaussian envelope of 1.5° SD. Noise was added to the

Gabor every trial to increase task difficulty. The noise was generated by smoothing

white noise with a Gaussian kernel (SD = 0.91°) and then combined with the Gabor at

a ratio of 3:1. Thus, a 25% -contrast Gabor was added to 75% noise. All possible Gabor orientations were presented. Another set of noise was generated using the same parameters to mask visual aftereffects after Gabor offset. The visual stimulus was presented 6.5° to the right of fixation at the center of the screen.

Vowels and auditory noise were synthesized following parameters in Experiment 1.3. Briefly, vowels were synthesized and morphed along a circular continuum with the vowel sounds /u:/, /ɜ:/, and /ɑ:/ as anchors (Figure 1.4.1 a) using a modified *vowel* function from the MATLAB audio toolkit (S. Smith, 2011). We synthesized the vowels at a fundamental frequency of either 122 Hz (Experiment 1.4 & 1.5) or 120 Hz (Experiment 1.6) at a sampling rate of 44.1 kHz. Auditory noise were generated by scrambling the morphed vowels.

The term *stimulus vowel* denotes vowels heard at the onset of the multimodal stimulus and *response vowel* denotes vowels heard during response phase. In Experiments 1.4 and 1.5, the stimulus vowels were 2 Hz higher than the response vowels, whereas in Experiment 1.6, both the stimulus and response vowels had the same pitch.

During the response phase, participants had to either respond to the Gabor orientation or the vowel morph. Visual responses to orientation were made by using a computer mouse to adjust the orientation of a white bar (width = $.61^\circ$, length = 1.5°) at the same location as the previously presented Gabor. Auditory responses to vowels were made by adjusting a response vowel which morphed in real time when the computer mouse moved. The white bar and the response vowels were never presented concurrently. The initial bar orientation or response vowel morphed step were randomized on every trial.

In Experiment 1.6, participants did not make responses during no-response trials. The duration until the next trial in no-response trials was determined by the participant's average response time since the start of the block.

1.4.3: Procedure for experiment 1.4

The experiment was conducted in a dim room. Participants rested their head on the chin rest and wore headphones. They were instructed to maintain fixation throughout the experiment. There were two conditions: Visual (V) and Auditory (A), corresponding to the response modalities. Participants matched either the adjustment bar to the Gabor orientation (V), or the response vowel to the stimulus vowel (A) as quickly and as accurately as possible. The stimulus was always multi-modal. Participants were randomly assigned to start with either condition. They completed both conditions over two separate visits.

Conditions V and A were divided into four blocks of 104 trials per condition (416 trials in total). There was a five-minute rest time after each block. Participants were encouraged to rest longer if needed before proceeding with subsequent blocks. Each condition lasted roughly 1h 30 mins with rests.

Before the experiment started, participants performed 40 training trials. Participants selected either condition for practice by pressing a key. Feedback was provided at the end of each training trial. Training data were excluded from the analysis.

1.4.3.1: Procedure for experiment 1.5

The procedure for Experiment 1.5 was identical to Experiment 1.4 except for the following: Participants were instructed to pay attention to both stimulus modalities. The response modality was randomized on every trial using a uniform distribution. On any given trial, participants did not know which modality to report until the response

phase. During the response phase, participants were to respond to the stimulus orientation if they saw the adjustment bar, or to respond to the stimulus vowel if they heard the response vowel. Participants were familiar with the task and the stimulus because they completed Experiment 1.4 before Experiment 1.5. Experiment 1.5 comprised eight blocks of 104 trials (832 trials in total). On average, there were 52 (50%) visual trials and 52 (50%) auditory trials per block.

1.4.3.2: Procedure, experiment 1.6

The procedure for Experiment 1.6 was identical to Experiment 1.5 except for the following: Participants familiarized themselves with the stimulus and task by completing 30 training trials (discarded from the analysis). Participants were then briefed about no-response trials prior to the start of the experiment. During no-response trials, the adjustment bar or the adjustment vowel were not presented. Participants completed 10 blocks of 102 trials (1020 trials total per participant). On average, there were 20 (20%) no-response trials, 41 (40%) visual trials, and 41 (40%) auditory trials.

1.4.4: Analysis and general descriptions

The analysis was conducted in MATLAB (Mathworks Inc., Natick, MA, USA) using the curve fitting toolbox. We used the circStat toolbox to calculate angular statistics (Berens, 2009). To investigate serial dependence for reports of each modality in Experiment 1.4, we looked at whether stimulus history influenced the response errors. The analysis followed that used by J. Fischer and Whitney (2014). Response errors were calculated by subtracting response orientations from the stimulus orientations. Positive errors meant that participants responded more clockwise to the stimulus. Errors larger than 90° were remapped in the opposite direction. Trials with

response times longer than 15 s (for visual responses) and 20 s (for auditory responses) were discarded from the analysis.

N-back histories were calculated by subtracting the current stimulus orientation from the stimulus orientation of the n^{th} previous trial. We computed histories for up to $n = 5$ for Experiment 1.4, but only analyzed 1-back histories for Experiments 1.5 and 1.6. Responses were pulled toward the direction of the n^{th} stimulus if both the n^{th} stimulus and response errors were in the same direction (e.g., clockwise).

1.4.4.1: Means-subtraction and raw-subtraction descriptions

An observer may have pre-existing bias prior before responding to the stimulus. We can remove these biases by centering the data across participants. This step also allows us to compare responses across modalities. We conducted two bias-subtraction methods. Using either bias-subtraction methods did not significantly affect the results. In the first method, the mean-subtraction method, we centered trial response errors by subtracting them from the mean response error in each condition (Experiment 1.4) or from the mean response errors of the same response modality (Experiments 1.5 & 1.6).

In the second method, the raw-subtraction method, data was centered by subtracting biases from the raw responses for each stimulus value. We subtracted biases from the raw responses using the following procedure. Participants were accurate if their responses fell along the unity line (i.e. response = stimulus). To determine the amount of biases contained in each response, we first calculated the distance between the raw responses and the unity line for each stimulus. We then computed the mean of the distance for each respective modality and subtracted the mean from the raw responses. This removed any response biases. After subtraction,

we remapped data in the opposite direction if they fell outside 0° – 180° due to the calculations. We then repeated the serial dependence analysis on this data.

1.4.4.2: Serial dependence analysis

We visualized serial dependence by binning the response errors using a rolling averaging window (bin width = 15°). The magnitude of serial dependence was quantified by the amplitude parameter of the derivative of Gaussian (DoG) curve. A positive amplitude represents an attractive serial dependence bias, whereas a negative amplitude illustrates a repulsive bias. For simplicity, we report only positive amplitude values while describing the direction of the bias (i.e. attractive or repulsive).

For Experiments 1.5 and 1.6, we analyzed serial dependence separately depending on the modalities reported in the current and previous trials. All the analyses were abbreviated accordingly. For instance, in Experiment 1.5, VA refers to pairs where the current trial was A and the previous trial V. In Experiment 1.6, we use N for no-responses trials. The notation NV denotes pairs where the current trial was V and the previous trial was a no-response trial.

1.4.4.3: Fixed effects analysis and hypothesis testing

We conducted fixed effects analysis for all experiments to measure serial dependence at the group level (Fritsche et al., 2017). We pooled the raw responses and stimuli from all participants in the respective conditions and experiments. Significance testing was carried out on the group data using a permutation test described previously (see Experiment 1.3).

For each permutation iteration, we computed the group response errors, n-backs, and centered the response errors based on the corresponding conditions (Experiment 1.4) or response modalities (Experiments 1.5 & 1.6). For each shuffled iteration, the empirical width of the visual condition and the auditory condition in

Experiment 1.4 was used to constrain the w parameter of DoG fits for each respective modality in Experiments 1.5 & 1.6 to perform bootstrap significance testing at the group level. The resulting distribution of fitted amplitude values was used to construct 95% confidence intervals (B. Efron & Tibshirani, 1986).

Significant empirical amplitudes were detected if values fell outside this confidence interval. We also performed Bonferroni correction to account for multiple comparisons in both experiments (Abdi, 2007). With an alpha value of .05, the cutoff for each experiments were: Experiment 1.4, $p < .01$ per condition for comparisons up to 5-backs, Experiment 1.5, $p < .0125$ (VV, AA, VA, & AV), and Experiment 1.6, $p < .0083$ (VV, AV, NV, AA, VA, & NA).

We reported the bootstrapped standard error of means (SEM) and the 95% confidence intervals for all analyses. In addition, we calculated exact partial eta-squared (η_p^2) effect sizes across the analyses, regardless whether the permutations were significant. This was achieved by comparing the empirical amplitude with the permuted amplitudes. This calculation determined how much the empirical amplitude was present when compared to a randomly shuffled sample.

Results

1.4.5: Descriptive statistics

We visualized response accuracy for all experiments using a scatter plot of the raw responses against stimuli (Figure 1.4.2 for mean subtraction and 1.4.2.1 for raw subtraction). Responses were noisy, but centered around the unity line (i.e., response = stimulus), indicating that in general, participants were accurate at performing the task. There were no obvious biases in visual responses. For auditory responses, there were three clusters (Figure 1.4.2b, d, & f) representing the three canonical vowels, meaning

that subjects were biased to respond closer to a canonical vowel than to the morphed stimulus.

Figure 1.4.2 Plot of raw responses against stimulus for all experiments. a), c), e) Raw visual response plots, b), d), f) Raw auditory response plots. The diagonal line represents the unity line. In b), d), & f), the ovals mark the three clusters corresponding to the three canonical vowels /u:/, /ɜ:/, and /ɑ:/

This bias did not affect the analysis of serial dependencies, because the permutation analysis creates empirical null distributions that include the same

canonical bias. If the clustering around canonical values could somehow cause a serial dependence bias, it would also be reflected in permuted iterations. We also subtracted systematic biases from the raw responses before analyzing serial dependence. This analysis from the raw-subtraction data did not produce qualitatively different results (Figure 1.4.2.1).

Figure 1.4.2.1. Raw responses as a function of stimulus after subtracting biases in the raw responses. a), c), e) Raw visual response plots, b), d), f) Raw auditory response plots. The diagonal line represents the unity line. Compared to Figure 1.4.2 (b, d, & f), the canonical vowels in the auditory responses were removed with this subtraction method.

Trials with response times exceeding 15 s (for visual responses) and 20 s (for auditory responses) were removed. In total, 15 (.19%) trials from Experiment 1.4, and 11 (.19%) trials from Experiment 1.5 were removed. In Experiment 1.4, participants were significantly quicker at visual responses (Mean RT = 3.02 s, SD = 0.70 s) than auditory responses (Mean RT = 4.67 s, SD = 2.10 s), $t(18) = 44.62$, $SD = .16$, $p = 6.94 \times 10^{-20}$. Participants also made statistically smaller errors when making visual responses (Mean magnitude = 14.10, SD = 4.49), than auditory responses (Mean magnitude = 32.93, SD = 5.34), $t(18) = -10.59$, $SD = 7.75$, $p = 3.66 \times 10^{-9}$.

Reaction times for Experiment 1.5 were shorter when reporting visually (Mean RT = 3.30 s, SD = 0.63 s) than to A (Mean RT = 4.36 s, SD = 0.61 s), $t(6) = -3.01$, $SD = .92$, $p = .024$. Participants made significantly smaller errors when making visual reports (Mean magnitude = 14.51, SD = 2.60) than to auditory reports (Mean magnitude = 32.78, SD = 6.92), $t(6) = -5.85$, $SD = 8.26$, $p = .001$.

In Experiment 1.6, participants were also statistically faster at visual responses (Mean RT = 3.18 s, SD = 0.28 s) than auditory responses (Mean RT = 4.54 s, SD = 0.77 s), $t(9) = -7.59$, $SD = .57$, $p = 3.35 \times 10^{-5}$. Moreover, participants made substantially smaller response errors to visual reports (Mean magnitude = 15.33, SD = 4.25) than to auditory reports (Mean magnitude = 35.97, SD = 6.67), $t(9) = -14.14$, $SD = 4.61$, $p = 1.88 \times 10^{-7}$.

1.4.5.1: Experiment 1.4 means-subtraction shows visual but not auditory serial dependence

To test for serial dependence, we examined whether response errors were attracted toward stimuli from previous trials. When the orientation from the previous trial was more clockwise than in the current trial, serial dependence would predict a clockwise response error, and vice versa. We visualized the data by plotting response

errors as a function of the change of stimulus orientation. The amplitude parameter of a fitted DoG model quantified serial dependence. Table 1.4.1 shows the bootstrapped error estimates and effect sizes for mean subtraction results in Experiment 1.4.

Table 1.4.1 Experiment 1.4 means, bootstrapped error estimates, confidence intervals, and effect sizes for mean subtraction results

N-back	Visual-only (V)		Auditory-only (A)	
	Error estimates	η_p^2	Error estimates	η_p^2
1-back	$1.53^\circ \pm .17^\circ (-.57^\circ-.92^\circ)$	.86	$.81^\circ \pm .08^\circ (-3.75^\circ-3.64^\circ)$	.07
2-back	$.85^\circ \pm .17^\circ (-.58^\circ-.91^\circ)$	.61	$.75^\circ \pm .09^\circ (-3.83^\circ-3.63^\circ)$	.09
3-back	$1.39^\circ \pm .16^\circ (-.58^\circ-.89^\circ)$	.84	$1.28^\circ \pm .11^\circ (-3.78^\circ-3.57^\circ)$	.16
4-back	$.42^\circ \pm .17^\circ (-.57^\circ-.92^\circ)$	.18	$.27^\circ \pm .03^\circ (-1.34^\circ-1.27^\circ)$	.06
5-back	$.04^\circ \pm .17^\circ (-.55^\circ-.90^\circ)$	.13	$.18^\circ \pm .02^\circ (-1.31^\circ-1.25^\circ)$	.03

In Experiment 1.4, we found serial dependence in the visual condition. For each n-back history, the shape of the rolling means resembled the typical serial dependence function. Group responses were pulled toward the previous stimulus by 1.53° , $R^2 = .74$, $RMSE = .010$, for 1-back (Figure 1.4.3a), 0.85° , $R^2 = .61$, $RMSE = .009$, for 2-back (Figure 1.4.3b), and 1.39° , $R^2 = .85$, $RMSE = .007$, for 3-back histories (Figure 1.4.3e). The DoG curve was flat and a bad fit for 4-back, $R^2 = .02$, $RMSE = .011$, and 5-back, $R^2 = .0004$, $RMSE = .013$. Permutation tests revealed that serial dependence was significant for 1-back and 3-back histories, but not 2-back histories ($p_{1\text{-back}} = .0002$, $p_{2\text{-back}} = .041$, $p_{3\text{-back}} = .0005$, Bonferroni-corrected $\alpha = 0.01$).

Figure 1.4.3. Serial dependence results of Experiment 1.4. Response errors as a function of stimulus history for 1-back (a) and 2-back (b) in visual condition, and response errors in auditory condition (c and d). The x-axis represented the difference between the stimulus orientation in the n^{th} previous trial and the stimulus orientation in the current trial. The average was calculated using a 15° binning window. The grey areas demarcate the SEM. The blue lines indicate a fitted derivative-of-Gaussian (DoG) curve. e) shows amplitudes of fitted DoG curves for up to 5-back across both conditions. Error bars represent 1 SEM of the permutation distribution.

For the auditory condition, auditory response errors as a function of stimulus history revealed no evidence for serial dependence (Figure 1.4.3c, d, & e). Group responses were pulled toward stimulus history by 0.75° , $R^2 = .30$, $\text{RMSE} = .013$, at 2-

back (Figure 1.4.3d). Group responses were repelled by 0.27° , $R^2 = .06$, $RMSE = .012$, at 4-back and by 0.18° , $R^2 = .001$, $RMSE = .014$, at 5-back histories. The DoG curve was irregular for 1-back, $R^2 = .03$, $RMSE = .017$ (Figure 1.4.3d) and 3-back, $R^2 = .12$, $RMSE = .012$, histories. Permutation tests revealed no significant auditory serial dependence ($p_{1\text{-back}} = .67$, $p_{2\text{-back}} = .69$, $p_{3\text{-back}} = .49$).

1.4.5.2: Experiment 1.4 raw-subtraction shows visual but not auditory serial dependence

Table 1.4.1.1 shows the bootstrapped error estimates and effect sizes for raw subtraction results in Experiment 1.4. For the visual condition, group responses were pulled toward the previous stimulus by 1.18° , $R^2 = .74$, $RMSE = .008$, for 1-back (Figure 1.4.3.1a), 0.61° , $R^2 = .35$, $RMSE = .009$, for 2-back (Figure 1.4.3.1b), and 0.94° , $R^2 = .71$, $RMSE = .008$, for 3-back histories (Figure 1.4.3.1e). The DoG curve was flat and a bad fit for 4-back, $R^2 = .005$, $RMSE = .012$, and 5-back, $R^2 = .07$, $RMSE = .008$. Permutation tests revealed that serial dependence was only significant for 1-back histories ($p_{1\text{-back}} = .0032$, $p_{2\text{-back}} = .14$, $p_{3\text{-back}} = .02$, Bonferroni-corrected $\alpha = 0.01$).

Table 1.4.1.1 Experiment 1.4 means, bootstrapped error estimates, confidence intervals, and effect sizes for raw subtraction results

N-back	Visual-only (V)		Auditory-only (A)	
	Error estimates	η_p^2	Error estimates	η_p^2
1-back	$1.18^\circ \pm .18^\circ (-.57^\circ-.92^\circ)$	.78	$.60^\circ \pm -.07^\circ (-3.85^\circ-3.65^\circ)$	.06
2-back	$.61^\circ \pm .17^\circ (-.57^\circ-.92^\circ)$	.40	$.71^\circ \pm -.09^\circ (-3.79^\circ-3.60^\circ)$	.08
3-back	$.94^\circ \pm .17^\circ (-.56^\circ-.92^\circ)$	.67	$.60^\circ \pm -.06^\circ (-3.71^\circ-3.58^\circ)$	.06
4-back	$.36^\circ \pm .17^\circ (-.56^\circ-.92^\circ)$	.11	$.93^\circ \pm -.11^\circ (-4.10^\circ-3.84^\circ)$	.08
5-back	$.74^\circ \pm .17^\circ (-.56^\circ-.92^\circ)$	.53	$1.79^\circ \pm -.09^\circ (-4.09^\circ-3.88^\circ)$	.31

Figure 1.4.3.1. Serial dependence results of Experiment 1.4 after subtracting from raw responses. a) & b) Response errors as a function of stimulus history in the visual condition. The x-axis represented the difference between the stimulus orientation in the n^{th} trial and the stimulus orientation in the current trial. The average was calculated using a 15° binning window. The blue line indicated the fitted derivative-of-Gaussian (DoG) curve. The grey area demarcated the SEM. c) & d) as a) & b) for auditory condition.

For the auditory condition, auditory response errors as a function of stimulus history revealed no evidence for serial dependence (Figure 1.4.3.1b, d, & e). Group responses were pulled toward stimulus history by 0.60° , $R^2 = .32$, $\text{RMSE} = .011$, at 3-

back. Group responses were repelled by 0.93° , $R^2 = .35$, $RMSE = .013$, at 4-back. The DoG curve was flat and a bad fit for 1-back, $R^2 = .02$, $RMSE = .018$, 2-back, $R^2 = .10$, $RMSE = .009$, and 5-back, $R^2 = .20$, $RMSE = .012$, histories. Permutation tests revealed no significant auditory serial dependence ($p_{1\text{-back}} = .76$, $p_{2\text{-back}} = .71$, $p_{3\text{-back}} = .75$).

From Experiment 1.4, we found significant serial dependence for the visual task for 1-back and 3-back histories. Responses in the auditory task were much more varied and not well captured by a DoG curve indicating serial dependence.

1.4.5.3: Experiment 1.5 means-subtraction show visual serial dependence within and across modalities

Experiment 1.5 was designed to test whether serial dependence occurred even when participants did not know in advance which modality to report from trial to trial. Participants had to pay attention to both stimulus modalities during each trial because the task modality was only known during the response phase. We first determined whether there was serial dependence for successive trials of the same modalities (VV & AA). Only 1-back histories were tested. Table 1.4.2 shows the bootstrapped error estimates and effect sizes for mean subtraction results in Experiment 1.5.

Table 1.4.2 Experiment 1.5 means, bootstrapped error estimates, confidence intervals, and effect sizes for mean subtraction results

N-back	Error estimate	η_p^2
VV	$2.43^\circ \pm .12^\circ (-1.68^\circ - 1.96^\circ)$	.76
AV	$2.91^\circ \pm .13^\circ (-1.65^\circ - 1.92^\circ)$	.82
AA	$5.44^\circ \pm .01^\circ (-8.98^\circ - 8.63^\circ)$	.41
VA	$4.65^\circ \pm .22^\circ (-8.67^\circ - 9.25^\circ)$	.32

Group results revealed the presence of serial dependence. Visual responses were pulled toward the stimulus of the previous trial by 2.43° , $R^2 = .79$, $RMSE = .014$ (Figure 1.4.4a). For auditory responses, the DoG curve was flat and poorly fitted, $R^2 = .17$, $RMSE = .042$ (Figure 1.4.4b). Permutation tests revealed evidence of serial dependence for VV ($p_{VV} = .0107$, Bonferroni-corrected $\alpha = .0125$).

We then examined whether serial dependence was present when participants responded to different modalities for successive trials (VA & AV). Group results revealed the presence of serial dependence for V responses only. V responses on the current trial were pulled toward stimulus history by 2.91° , $R^2 = .84$, $RMSE = .014$ (Figure 1.4.4c). The DoG curve was flat and poorly fitted for VA, $R^2 = .18$, $RMSE = .033$ (Figure 1.4.4d). Permutation tests indicated significant serial dependence for AV ($p_{AV} = .0021$, Bonferroni-corrected $\alpha = .0125$).

Figure 1.4.4. Serial dependence results of Experiment 1.5. a) & b) Response errors as a function of stimulus history for 1-back trials with the same response modalities (VV and AA). c) & d) response errors for 1-back trials with different response modalities.

1.4.5.4: Experiment 1.5 raw-subtraction show visual serial dependence within and across modalities

Table 1.4.2.1 shows the bootstrapped error estimates and effect sizes for raw subtraction results in Experiment 1.5. For successive trials of the same modalities, V responses were pulled toward the stimulus of the previous V trial by 2.22° , $R^2 = .62$, $RMSE = .018$ (Figure 1.4.4.1a). The DoG curve was flat and poorly fitted for auditory responses, $R^2 = .02$, $RMSE = .034$ (Figure 1.4.4.1b). Permutation tests revealed evidence of serial dependence for VV ($p_{VV} = .006$, Bonferroni-corrected $\alpha = .0125$).

Table 1.4.2.1 Experiment 1.5 means, bootstrapped error estimates, confidence intervals, and effect sizes for raw subtraction results

N-back	Error estimate	η_p^2
VV	$2.22^\circ \pm .01^\circ (-1.56^\circ - 1.57^\circ)$	.79
AV	$3.08^\circ \pm .01^\circ (-1.59^\circ - 1.58^\circ)$	.88
AA	$1.56^\circ \pm .01^\circ (-7.28^\circ - 7.30^\circ)$	.08
VA	$8.69^\circ \pm .02^\circ (-7.50^\circ - 7.32^\circ)$	.72

Across modalities, group results (AV) revealed the presence of serial dependence for V responses. V responses on the current trial were pulled toward stimulus history by 3.08° , $R^2 = .79$, $RMSE = .018$ (Figure 1.4.4.1c). The DoG curve was flat and poorly fitted for VA, $R^2 = .55$, $RMSE = .025$ (Figure 1.4.4.1d). Permutation tests indicated significant serial dependence for AV ($p_{AV} = .0001$, Bonferroni-corrected $\alpha = .0125$).

For Experiment 1.5, we found significant serial dependence when participants made visual responses. The effect was present regardless of the response modality in the previous trial. There was no serial dependence when participants made auditory responses.

Figure 1.4.4.1. Serial dependence results of Experiment 1.5 after subtracting from raw responses. a) & b) Response errors as a function of stimulus history for 1-back trials with the same response modalities (VV and AA). c) & d) response errors for 1-back trials with different response modalities (AV and VA).

1.4.5.5: Experiment 1.6 means-subtraction show serial dependence without responses

In Experiment 1.6, we further examined the task-dependence of serial dependence by also including 20% no-response trials. We compared whether the previous stimulus also influenced subsequent reports, if participants made no responses in the 1-back trial (NV & NA). Table 1.4.3 shows the bootstrapped error estimates and effect sizes for mean subtraction results in Experiment 1.6.

Table 1.4.3. Experiment 1.6 means, bootstrapped error estimates, confidence intervals, and effect sizes for mean subtraction results

N-back	Error estimate	η_p^2
NV	$4.33^\circ \pm .13^\circ (-2.37^\circ - 2.59^\circ)$	.84
NA	$5.03^\circ \pm .17^\circ (-13.43^\circ - 13.81^\circ)$	.20
VV	$2.48^\circ \pm .06^\circ (-1.67^\circ - 1.79^\circ)$	.79
AV	$1.32^\circ \pm .03^\circ (-1.68^\circ - 1.73^\circ)$	.52
AA	$9.14^\circ \pm .04^\circ (-9.20^\circ - 9.33^\circ)$	.65
VA	$9.47^\circ \pm .12^\circ (-9.04^\circ - 9.13^\circ)$	.67

Visual responses showed positive attraction toward stimulus history when participants did not respond in the previous trial (NV). Visual responses were pulled by 4.33° , $R^2 = .53$, $RMSE = .038$ (Figure 1.4.5a). The DoG curve was flat and poorly fitted for NA, $R^2 = .07$, $RMSE = .056$ (Figure 1.4.5b). Permutation tests found significant serial dependence for visual responses ($p_{NV} = .0009$, Bonferroni-correct $\alpha = .0083$).

We further examined if there was serial dependence when participants responded to the same modalities on successive trials (VV & AA), as in the previous two experiments. Visual responses were pulled toward stimulus histories by 2.48° , $R^2 = .36$, $RMSE = .031$ (Figure 1.4.5c). The DoG curve was flat and poorly fitted for AA, $R^2 = .33$, $RMSE = .047$ (Figure 1.4.5d). Permutation tests confirmed serial dependence in VV $p_{VV} = .004$ (Bonferroni-corrected $\alpha = .0083$).

We further analyzed serial dependence for responses from different modalities across successive trials (AV & VA). Group responses indicated evidence of serial dependence for AV. V responses on the current trial were attracted by 1.32° toward stimulus histories, although the fit was poor $R^2 = .24$, $RMSE = .026$ (Figure 1.4.5e).

The DoG curve was flat and poorly fitted for VA, $R^2 = .25$, $RMSE = .06$ (Figure 1.4.5f). Permutation tests did not reveal any significant effect ($p_{AV} = .13$).

Figure 1.4.5. Serial dependence results of Experiment 1.6. a), c), & e) Visual response errors as a function of 1-back histories. b), d), & f) Auditory response errors as a function of 1-back histories.

1.4.5.6: Experiment 1.6 raw-subtraction shows serial dependence without responses

Table 1.4.3.1 shows the bootstrapped error estimates and effect sizes for raw subtraction results in Experiment 1.6.

Table 1.4.3.1. Experiment 1.6 means, bootstrapped error estimates, confidence intervals, and effect sizes for raw subtraction results

N-back	Error estimate	η_p^2
NV	$4.08^\circ \pm .004^\circ$ (-2.28°–2.30°)	.86
NA	$2.79^\circ \pm .09^\circ$ (-11.80°–11.86°)	.10
VV	$1.93^\circ \pm .01^\circ$ (-1.60°–1.59°)	.74
AV	$1.08^\circ \pm .01^\circ$ (-1.62°–1.56°)	.48
AA	$4.88^\circ \pm .01^\circ$ (-8.15°–8.11°)	.41
VA	$.20^\circ \pm .10^\circ$ (-8.13°–8.37°)	.003

Visual responses showed positive attraction toward stimulus history when participants did not respond in the previous trial (NV). Visual responses were pulled by 4.08° , $R^2 = .50$, $RMSE = .037$ (Figure 1.4.5.1a). The DoG curve was flat and poorly fitted for NA, $R^2 = .05$, $RMSE = .046$ (Figure 1.4.5.1b). Permutation tests found significant serial dependence for visual responses ($p_{NV} = .0007$, Bonferroni-corrected $\alpha = .0083$).

For responses of the same modalities on successive trials (VV & AA), visual responses were pulled toward stimulus histories by 1.93° , $R^2 = .10$, $RMSE = .035$ (Figure 1.4.5.1c). The DoG curve was flat and poorly fitted for AA, $R^2 = .27$, $RMSE = .028$ (Figure 1.4.5.1d). There was no serial dependence ($p_{VV} = .018$, $p_{AA} = .24$, Bonferroni-corrected $\alpha = .0083$).

Figure 1.4.5.1. Serial dependence results of Experiment 1.6 after subtracting from raw responses. a), c), & e) Visual response errors as a function of 1-back histories. b), d), & f) Auditory response errors as a function of 1-back histories. N represents no-response trials.

For responses from different modalities across successive trials (AV & VA), V responses on the current trial were attracted by 1.08° toward stimulus histories, $R^2 = .22$, $RMSE = .023$ (Figure 1.4.5.1e). The DoG curve was flat and poorly fitted for VA, $R^2 = -.05$, $RMSE = .044$ (Figure 1.4.5.1f). Permutation tests did not reveal any significant effect ($p_{AV} = .18$, $p_{VA} = .96$).

From Experiment 1.6, we found significant serial dependence when participants did not respond in the previous trial. We also found the effect only when participants responded to the visual modalities on successive trials. There was no effect for auditory reports on the current trial if participants did not respond, reported auditory modalities, or reported visual modalities on the previous trial.

1.4.5.7: Evaluating the bias subtraction methods

In this section, we evaluate the differences between the two bias subtraction methods. There were three changes when subtracting bias from the raw responses. The first change was the 3-back serial dependence in Experiment 1.4 V condition was no longer significant ($p_{3\text{-back}} = .025$, Bonferroni-corrected $\alpha = .0167$). The second change was that the positive slope for Experiment 1.5 VA (Figure 1.4.4.1d) was significant when uncorrected, $p = .021$ (Bonferroni-corrected $\alpha = .0125$). Although the slope did not resemble serial dependence, it fitted well to the data, $R^2 = .55$, RMSE = .025. The third change was the lack of significant serial dependence for Experiment 1.6 VV (Figure 1.4.5.1c). V responses were attracted by 1.93° , $R^2 = .10$, RMSE = .035, toward 1-back histories. Permutation analysis showed that serial dependence was significant when uncorrected, $p = .018$ (Bonferroni-corrected $\alpha = .0083$). We concluded that these changes did not grossly influence the pattern of results.

Discussion

1.4.6: Visual serial dependence in a multimodal stimulus even when task expectations are violated

We investigated serial dependence by using a multimodal stimulus which contained more information to provide sensory estimates of the stimulus features and multiple ways to report them. In our stimuli, visual orientation of a grating was always consistently paired with a vowel sound from a morph wheel, providing redundant information to execute the task. In Experiment 1.4, we found compelling evidence for serial dependence when participants had to report the visual orientation. We did not find evidence for serial dependence or adaptation when the auditory feature was reported.

We then evaluated whether task expectations affected serial dependence in Experiment 1.5. Participants attended to both modalities but reported only one of them. The report modality was unknown to the participants because it was randomized on every trial, and only announced in the response phase of each trial. We found serial dependence when participants reported two successive trials in the visual domain. This bias was also present on the current visual report when participants made auditory reports in the trial before, but not vice versa.

Finally, we investigated whether serial dependence was evident when no-response trials were included in Experiment 1.6, in addition to randomizing tasks. There was serial dependence on the current visual response trial even if the trial was preceded by a no-response trial. Again, no serial dependence or adaptation effect was found for auditory response trials.

1.4.6.1: Serial dependence, an effect of perceiving the previous stimulus

Fritsche et al. (2017) argued that serial dependence appears at the decision level. The analysis and interpretation of serial dependence experiments were complicated by the meaning of ‘decision’. Serial dependence could be an effect *of* making decisions about the previous stimulus which subsequently influences how current stimulus is reported, or it could be an effect *on* making decisions about the current stimulus.

We showed that serial dependence was evident in visual responses even when participants made auditory reports in the preceding trial (AV). Furthermore, our stimulus was always multimodal and contained both features across our experiments. If serial dependence was an effect of making decisions about the previous trial, we should observe a strong effect when the task remained the same on the current trial (i.e., VV or AA). A weaker effect may be present, albeit less likely, if the task was different on the current trial (i.e., VA or AV). However, we measured serial dependence only when participants reported visual orientation, regardless of the response modality on the previous trial.

Previous studies have argued for a perceptual basis of serial dependence based on finding an effect after no-response trials (J. Fischer & Whitney, 2014; A. Liberman et al., 2014). No-response trials cannot fully justify whether serial dependence is perceptual or decision. Participants in those studies expect to perform a specific task. They might have already judged, internally, the stimuli immediately after presentation, regardless if they were subsequently asked to respond or not.

In Experiment 1.5, participants did not have a specific expectation to perform one task. Arguably, they only decide on a response once the response modality was revealed to them. Experiment 1.6 included additional no-response trials in the context

of a non-predictable task. Despite these additions, we showed that whether the previous trial included a response (and decision) of the same, different, or no modality at all, was irrelevant to the serial dependence bias. Only visual responses were subjected to serial dependence. This finding is also consistent with evidence for serial dependence in the absence of any tasks, using visually evoked potentials as dependent measures (Fornaciai & Park, 2018). This means that future experiments do not require the use of no-response trials as serial dependence bias, when found, continues to be present in the current trial.

When taken together, our evidence suggests that serial dependence is better characterised as an effect of perceiving the previous stimulus since no-response trials and trials with responses to a different modality produce the same serial dependence biases on subsequent reports. Capacity constraints make it unlikely that participants internally decide on two possible responses simultaneously. Whether the bias occurs at a perceptual or a decision level warrants further investigation.

1.4.6.2: Serial dependence and multimodal integration

Let us now consider whether the response bias is determined at a modality-specific level or after a multimodal integration stage. If serial dependence arises because a decision was made after a multisensory integration stage, then reports toward a multimodal stimulus should be biased regardless of the response modality on the previous or current trial. However, we did not find serial dependence of our multimodal stimulus when auditory information was used for reports. Instead, the effect was only apparent when participants reported visual information.

Does serial dependence bias occur in a multimodal stimulus? Our stimuli might not have led to strong multi-sensory integration because the mapping between vowel sounds and orientation was arbitrary. A recent report also failed to find serial

dependence across modalities. Auditory tones did not influence visual numerosity judgment in a serial dependence task (Fornaciai & Park, 2019). Other stimuli with a stronger correspondence between different modalities (e.g., pitch and size) might be used in future experiments to investigate multisensory integration of serial dependence.

1.4.6.3: Lack of auditory serial dependence

Similarity between stimuli is important in eliciting serial dependence. Cicchini et al. (2017) showed evidence of positive serial dependence only if participants were comparing similar stimuli. Likewise, A. Liberman et al. (2018) confirmed that serial dependence was only present when participants reported facial expressions within the same identity (i.e., same genders). In Experiment 1.4 and 1.5, there was a subtle difference between the pitch of the stimulus vowels and the response vowels of 2 Hz. It is possible that the vowels were too different to influence serial dependence. As such, one could argue that the vowels did not share the same identity. However, in Experiment 1.6, both stimulus and response vowels had the same pitch and we still did not find serial dependence for auditory reports.

The lack of auditory serial dependence in our study may be surprising. Recent studies have shown serial dependence in auditory feature judgments (Alais et al., 2015; Arzounian et al., 2017; Roseboom, 2019). For instance, Alais et al. (2015) presented a short gliding pitch to participants on every trial and asked them to indicate whether the sweep was an upward or downward glide. Participants were likely to report subsequent trials as unchanged when the previous pitch glided in the same direction.

Our stimuli employed only one specific auditory feature and adjustment space, a circular vowel morph wheel, which may have been a suboptimal choice in eliciting

serial dependence. However, in previous experiments (Experiment 1.1), we failed to find serial dependence for simple reports of pitch using the Method of Adjustment. Further, we aimed to use a circular adjustment space to remove artifacts related to linear adjustments (e.g. see Discussion in Experiment 1.1 & 1.2, and Experiment 1.3) so that we could achieve a one-to-one mapping between the visual and auditory modalities. We are not aware of previous studies reporting evidence for auditory serial dependence using Method of Adjustment or circular stimulus spaces. The lack of auditory serial dependence in our study may indicate that serial dependence is a strongly visual phenomenon.

We note that our auditory stimulus caused a strong bias to report canonical vowels; morphed vowels in between the original vowels used in creating the morphed stimulus space were less likely to be reported. While this bias might have increased the difficulty in finding auditory serial dependence by adding extra noise to the signal in our analysis, it should be independent of any additional serial dependence bias.

1.4.6.4: Timing is important for auditory serial dependence

Another commonality of most previous auditory serial dependence experiments is in the timing of stimuli and the time between responses. In Alais and colleagues' (2015) experiment, the duration from stimulus onset to the start of the response phase was only 100 ms. The duration of an entire trial was less than 2000 ms. In other serial dependence experiments involving auditory stimuli, the interval between stimulus onset and response was roughly 500 ms (Arzounian et al., 2017) and 1900 ms (Roseboom, 2019).

Timing plays an important role in serial dependence. J. Fischer and Whitney (2014) demonstrated that positive (attractive) or negative (repulsive) serial dependence can occur depending on the stimulus duration and the interval between two stimuli. In

our experiments, the interval between two multimodal stimuli was greater than 4000 ms. This was perhaps too long for auditory serial dependence. Since serial dependence for pitch was found when the stimulus duration and interval between the two stimuli was short, our current paradigm may not be sensitive enough to capture auditory serial dependence. Further examinations with shorter intervals between trials, without compromising serial dependence in vision, may be required.

1.4.6.5: Auditory serial dependence may be linked to working memory

An alternate explanation for the lack of auditory serial dependence in our current experiments could be related to working memory. Some literature indicates that auditory sensory memory lasts no more than ten seconds (Sams, Hari, Rif, & Knuutila, 1993). Auditory recognition memory is also shorter than visual recognition memory for the same stimulus length (M. A. Cohen, Horowitz, & Wolfe, 2009). Bliss et al. (2017) manipulated the ITI between trials and showed that serial dependence varied depending on the response time between the previous and the current trial. In their second experiment, they showed that an ITI of ten seconds resulted in a repulsive effect between the previous and the current response error. Thus, it is possible that the lack of auditory serial dependence in our experiment could be related to working memory.

1.4.6.6: Serial dependence and inconsistent analysis

A weakness of serial dependence experiments is the inconsistent analysis. Studies analyzed 1- (Fritsche et al., 2017), 3- (J. Fischer & Whitney, 2014), 4- (Manassi et al., 2018), and up to 5-backs (H. Zhang & Alais, 2018). In our experiments, we also analyzed n-backs of various sizes. The inconsistencies between n-backs may create suspicions that serial dependence is a statistical artifact. We now justify why we could not analyze up to 5-backs for all serial dependence experiments.

There were artifacts for Experiment 1.1 and 1.2. Simulated response errors which were noisy exhibited serial dependence. The simulated responses indicated the presence of artifacts. It would not be meaningful to analyze up to 5-backs for results with artifacts. Therefore, we did not proceed with further analysis unless the artifacts were removed.

In experiment 1.5 and 1.6, we investigated serial dependence by randomizing the response modalities during the response phase. Participants either made visual or auditory reports. At 5-back histories, there would be $P^R(5,2) = 25$ permutations in Experiment 1.5, and $P^R(5,3) = 125$ permutations in Experiment 1.6. For example, 5-backs could be VVVVVV, VVVVVA, VVVAVV, VVAVVV ... (V = visual, A = auditory).

The number of permutations for 5-back histories drastically reduces the amount of available trials per block for analysis. There are 104 trials per block. When we analyze 5-back histories, we are left with $104 - 5 = 99$ trials. This is not a problem if we only tested unimodal reports. When we factor in the permutations, such as getting the history VVAVA, the chance that this specific history was present in the experiment would be $= 1/125 * 99 = 0.792$ trials in Experiment 1.6. Participants completed $104 \times 4 = 416$ trials in total. This gives us $0.792 \times 4 = 3.168$ trials for the specific history VVAVA. To get enough power for analysis, participants would have to complete several hours of the experiment. Unfortunately, we do not have that many trials in our current data as each participant completed 416 trials total. Therefore, it was not possible to systematically analyze up to 5-backs across all experiments when response modalities were randomized.

1.4.6.7: Serial dependence and the natural environment

The attractive forces under serial dependence can be beneficial for interpreting the visual world. Objects in the real world do not change abruptly. Therefore, visual

biases of serial dependence enhance the permanence of objects in the natural setting. However, this does not apply equally to all visual features. Taubert, Alais, and Burr (2016) conducted an experiment testing the extent to which faces, and emotional expressions are influenced by serial dependence. In the experiment, participants had to judge the gender of a face (male/female) and its emotion (happy/sad). Taubert and colleagues (2016) showed that the responses to gender were subject to positive serial dependence (i.e., attractive responses). However, responses to emotion were repelled away from the previous response.

In their experiment, the visual stimulus provided both gender and emotional information. However, only the gender information succumbed to serial dependence. Taubert and colleagues (2016) argued that the attractive visual bias may not always be beneficial. The ability to detect a sudden change of emotion is important as emotions convey critical information about the current state of an individual. Moreover, it is unlikely that an individual abruptly changes their physical appearance during social interaction. This explains why gender, but not emotion, was subject to serial dependence bias.

The lack of an auditory effect in our results may be explained by a similar logic. Vowels sounds are constantly changing in human speech. When a word is articulated in English, the vowels are sometimes modified by the preceding consonants (De Jong, 1991). Detecting changes in vowels is crucial for understanding speech. An auditory bias which assimilates the current vowel to the previous vowel would be unfavorable and not provide many benefits to the intelligibility of the speech.

1.4.6.8: Interim summary

Recent debates on serial dependence circle about whether the effect is a perceptual or a decision-level bias. We conducted three experiments with a

multimodal audio-visual stimulus to further test the origins of the effect. We found serial dependence only when participants responded to the visual information across all the experiments. This effect was present when task expectations were eliminated, and when participants made no reports on the preceding trial. The presence of a previous visual stimulus alone was enough to elicit serial dependence, whether it was subject to attention or to a perceptual decision in a previous trial was irrelevant. Our results suggest that serial dependence is an effect of perceiving the previous stimulus.

General discussion for part 1

1.5.0: Sample size differences across serial dependence studies and the expected effect sizes and confidence intervals

Sample sizes vary across serial dependence experiments, between 2–25 participants (Cicchini et al., 2017; J. Fischer & Whitney, 2014; Fritsche et al., 2017). We calculated the expected effect size and power across our experiments using a non-directional two-tailed Cohen's d (J. Cohen, 1988). The formula was $d = |M_1 - M_2| \div s$, where M_1 = means from empirical data, $M_2 = 0$, and s = pooled standard deviation. The formula for pooled standard deviation was $s = \sqrt{\frac{SD_1^2 + SD_2^2}{2}}$, where SD_1 indicates SD from empirical data, and $SD_2 = 1$. We reasoned that if there was no serial dependence, then $M_2 = 0$ and $SD_2 = 1$. Thus, d indicated how big the effect of our study was, as compared to zero. Since existing serial dependence studies did not report effect sizes, we repeated the same analysis to compute effect sizes for existing studies.

Power analysis was not conducted because our studies were already completed. Post-hoc power analysis is often criticized as they provide misleading/non-meaningful information concerning the results. Instead, the literature recommends computing confidence intervals (Hoenig & Heisey, 2001; O'Keefe, 2007; Yuan & Maxwell, 2005; Y. Zhang et al., 2019). The sample sizes in our studies were small. Thus, we used t -values, instead of Z , to compute the confidence intervals. The formula for computing confidence intervals: $\bar{x} \pm t \times \frac{s}{\sqrt{n}}$, where $\bar{x}$ = sample mean, $s = SD$ and n = sample size. The value of t was taken from a t -distribution table for two-tailed distributions at $\alpha = .05$. This alpha level indicated a 95% chance to correctly reject a true null hypothesis. The 95% confidence intervals illustrated the range of values that would also be observed in the population with 95% certainty. To keep the reporting concise,

we used data from 1-back analyses. For Experiments 1.4–1.6, we used data from the mean-subtraction method.

1.5.1: Results for expected effect sizes and confidence intervals

Table 1.5 shows the expected effect sizes, means, and 95% confidence intervals between existing studies and our experiments. In general, Experiments 1.4–1.6 had large effect sizes. However, large effect sizes did not signify that serial dependence effect was also observed in the population. When the 95% confidence interval included null (i.e. 0), it suggested that the observed effects were unlikely occurring in the population. Therefore, we could not reject the null hypothesis.

Table 1.5. Effect size and 95% confidence intervals between current experiments and existing studies

Experiment 1.3			Existing Studies			
<i>d</i>	N	Means (C.I.)	<i>d</i>	N	Means (C.I.)	
.02	12	.95° (-38.88 – 40.78)	a)	7.67	4	6.76° (5.31 – 8.21)
			b)	1.26	25	1.17° (.82 – 1.52)
			c)	.57	16	.8° (-.10 – 1.70)
Experiment 1.4, Visual condition						
1.55	19	1.53° (1.06 – 2.00)				
Experiment 1.5, VV						
.93	7	2.43° (-.87 – 5.73)				
Experiment 1.6, NV						
1.73	10	4.33° (1.90 – 6.76)				

d = non-directional effect size using Cohen's *d*, N = number of participants, C.I. = 95% confidence intervals. Computed effects and C.I. in existing studies for a) experiment 1 in Fischer & Whitney (2014), b) experiment 1 in Fritsche et al., (2017), and c) experiment 1 in Cicchini et al, (2017).

1.5.2: Serial dependence as a functional unit of temporal stability

Serial dependence could be an expression of temporal stability. Serial dependence is a response bias in which the previous visual percept biases the current

visual response. Since there is already a broad scope of where serial dependence can occur, such as cell populations and working memory, it implicates serial dependence as an expression of temporal stability to achieve perceptual continuity. Under this assumption, our understanding of temporal stability changes from a catch-all mechanism to one with more concrete operations. Specifically, during evaluation between information, the previous information can bias the current information.

We speculated that the reason why visual serial dependence persisted, even when participants made auditory reports, involved a current perspective of perceptual continuity: hysteresis. Hysteresis of the visual information on trials where participants made auditory reports or made no reports was carried over to the subsequent visual report trial. By this logic, the persistent visual information endured by hysteresis could indicate how perceptual continuity is maintained when temporal stability evaluates information. It is important to address that J. Fischer and Whitney (2014) have shown that serial dependence is not hysteresis. Therefore, there should be no confusion because what we are describing is how hysteresis could aid in temporal stability.

1.5.3: Temporal stability is modality-specific, less so a serial effect

We previously postulated that temporal stability could be achieved either by integrating the previous and the current information or by discarding one of them and assigning the other as the continuous information. We then conducted several serial dependence experiments to determine if this was true. From our testing, we found that only visual information exhibited serial dependence. Visual serial dependence remained prominent regardless of what happened previously. Specifically, participants showed serial dependence in their visual responses even if they previously made auditory reports or made no reports. Therefore, our results indicated that temporal stability, when expressed using serial dependence, is modality-specific.

Temporal stability is unlikely a serial effect. Rather, it may manifest serial dependence. When this happens, previous information can bias current information to form a more continuous environment. The ability for temporal stability to express serial dependence does not prove that temporal stability is a kind of serial effect. For instance, temporal stability could be a failure in change detection. Change detection is a process of comparing changes between the previous and current information. When changes are undetected, perception is temporally stable. It is possible for the previous information to bias the current information, but we have no evidence to show this. Since we do not yet know the exact details of the evaluation process, we hesitate to argue that temporal stability is a serial effect.

The efforts of part 1 led to an expanded understanding of temporal stability. Temporal stability is no longer a vague mechanism that compares information. Serial dependence can be an expression of temporal stability. Under this assumption, the current visual information can be biased by the previous visual information. Meanwhile, temporal stability is also likely to be modality-specific. The information under comparison must be from the same modality because the current visual responses become biased by previous visual information. Since we only demonstrated evidence of temporal stability in visual responses, we limited our subsequent investigations in the remaining thesis to the visual domain.

Part 1 conclusion

Part 1 questioned if temporal stability was a serial effect. This was based on the similarities between the definition of temporal stability and serial dependence. Serial dependence is a serial effect in which the current response is biased by the previous stimulus. Serial dependence is also predominantly investigated in vision. Therefore, we conducted several experiments to test if there was auditory serial

dependence. However, we failed to find auditory serial dependence in our experiments.

Recent debates surrounding serial dependence called into question the nature of this bias: is serial dependence a perceptual or decision bias? We contributed to this debate by using a multimodal audio-visual stimulus. Results using the multimodal stimulus illustrated serial dependence for visual but not auditory reports. From these experiments, we concluded that in vision, serial dependence occurs in some aspects of vision because some features benefit from integrating previous and current visual signals. This integration helps us form a more stable visual environment.

Our findings in part 1 improved the current definition of temporal stability. Temporal stability is no longer a vague mechanism which compares information to determine if there is perceptual continuity. Temporal stability, when expressed through serial dependence, may influence current visual perception such that the percept becomes biased by the previous visual information. Temporal stability is modality-specific. Temporal stability may also involve other mechanisms which help maintain perceptual continuity.

Part 2: Comparing across endogenously elicited disruptions during blinks**2.0.0: Introduction to part 2**

Part 1 of the thesis highlighted the likelihood that temporal stability is modality-specific. Therefore, the remaining thesis limits investigation to the visual domain. The visual environment suffers from endogenously elicited disruptions in the form of eye blinks. We blink about 12–20 times per minute (Bentivoglio et al., 1997; Griepentrog & Lucarelli, 2011; Karson, 1983; Karson et al., 1981). When we blink, the eyelids cover the eye. There is blackness as no visual input is entering the eyes. According to temporal stability, we would constantly experience perceptual discontinuities after every blink because the blackness during the blink already differed from the percept of the environment from before the blink. However, this is not true. We do not feel as if the perceptual world is in chaos after each blink.

It is possible that temporal stability ignores the endogenous changes elicited by blinking. The perceptual system discards modality-specific information from the blink and compares the percept from before the blink to those from after the blink. Therefore, this reasoning suggests that temporal stability is a failure of change detection. Temporal stability is achieved because no changes were detected between percepts across blinking. Could the failure of detecting changes be at the core of temporal stability? To understand this, we must first realize why humans blink so often but do not experience disruptions after blinking. Then, we must comprehend how an observer fails to detect changes and what reasons lie behind this failure.

If temporal stability is a failure of detecting changes, and that it ignores endogenous disruptions from the blink, what happens to the fixation of an object if the object changes position during the blink? Changes to an object's position are undetected across a blink. This is demonstrated in blink adaptation, in which our gaze

after blinking is oriented towards an object's new position. We used blink adaptation to investigate oculomotor behaviors that could maintain perceptual continuity across blinks. We measured observers' eye positions when they looked at a stimulus but were unaware that the stimulus was displaced during a blink. We then showed how blink adaptation can maintain perceptual continuity by minimizing positional errors during the blink. From this finding, we speculated that temporal stability is not merely a failure of change detection. Rather, temporal stability is successful because other systems (i.e. the oculomotor system) are involved. We then speculated that there could be a signal which anticipated eye positions after blinking. This signal could be important when maintaining temporal stability.

In the next few sections, we first reviewed the reasons we blink and how blinks may play a role in perceptual continuity. Then, we briefly discussed *Change Blindness*, a phenomena where changes in a scene are undetected, to understand how observers fail to detect changes.

2.0.1: Physiological reasons for blinking

There are physiological reasons for blinking. We blink to protect the surface of our eyes. When we blink, the tear ducts open when the eyelid covers the eye to secrete tears (Doane, 1981; Tsubota, 1998). The tear is smeared across the ocular surface of the eye by the lid to form the tear film. At the same time, the meibomian glands secrete a layer of holocrine lipids which are evenly distributed on top of the tear film. The lipid layer provides structural integrity which prevents the film from evaporating quickly, protects the ocular surface from contamination, and allows the ocular surface to refract light (P. J. Driver & Lemp, 1996).

Blinking improves visual acuity when the eyes become dry. Vision gets blurred and loses acuity when the eyes are dry (Goto, Yagi, Matsumoto, & Tsubota, 2002;

Toda, Fujishima, & Tsubota, 1993). Dry eyes are caused by tear film evaporation or breakage and are uncomfortable (Himebaugh, Begley, Bradley, & Wilkinson, 2009). The discomfort provokes us to blink which, in turn, revitalizes the film. The refreshed film structure properly refracts light and sustains visual acuity.

A change in temperature/humidity also causes us to blink. The humidity across the ocular surface changes if we open our eyes for too long, such as when looking at a monitor (Tsubota & Nakamori, 1993). Cold thermoreceptors located at the ocular surface are activated when the surface is cooler than ambient. These receptors elicit pain signals, giving a sense of dryness and unpleasantness in the eyes (Belmonte & Gallar, 2011). Therefore, we blink to reduce temperature differences (Nakamori, Odawara, Nakajima, Mizutani, & Tsubota, 1997).

2.0.1.1: Blinking and the brain

Blinking is related to cognition and dopamine. Parkinsonian patients exhibit decreased spontaneous blink rates due to low dopamine (Karson, 1983). Cornea reflex, a blink reflex when the ocular surface is stimulated by foreign agents (Hiraoka & Shimamura, 1977), is reduced in Parkinsonian patients (Agostino, Berardelli, Cruccu, Stocchi, & Manfredi, 1987). Animal models for Parkinson's have confirmed that cornea reflex is reduced when dopamine levels are low (Lawrence & Redmond, 1991). Patients not on dopamine treatments have reduced blink rates (Agostino et al., 2008).

Blinks can express information processing. Short and brisk blinks occur at specific intervals while completing tasks (Fogarty & Stern, 1989). When we read, we blink at specific occasions such as when moving to a new line, or when making a saccade (Orchard & Stern, 1991). Blink frequency decreases during demanding tasks (Holland & Tarlow, 1972, 1975), and increases for divergent thinking (Chermahini & Hommel, 2010; Ueda, Tominaga, Kajimura, & Nomura, 2016).

In summary, there are physiological and cognitive reasons why we blink so frequently. Blinking helps protect our eyes from foreign agents by establishing the tear film. Blinking restores tear films and sustains visual acuity. Blinking is also an expression of cognition and information processing. Therefore, physiological, and cognitive factors propel us to blink frequently.

2.0.2: Eye blinks and perceptual continuity

There are three types of eye blinks: spontaneous, voluntary, or reflexive. Each type have unique characteristics that differ from each other (Kaneko & Sakamoto, 1999). Voluntary blinks are executed at will, by command, or when cued. Reflexive blinks are elicited by startling stimulus such as loud beeps (Silverstein, Graham, & Bohlin, 1981) or external stimulation (Evinger, Manning, & Sibony, 1991; Kaneko & Sakamoto, 1999). We often make these types of blinks but do not experience disruptions to the visual world.

Disruptions are the “darkness” which should arise when the eyelids cover the eye. Visual information is absent during the blink because the eyelid blocks information from entering the eyes. It takes about 200–350 ms for the eyelids to close and open when blinking (Guitton, Simard, & Codère, 1991; Stern, Walrath, & Goldstein, 1984). This duration increases for larger blinks and it is agreed that the lids take twice as long, or more, to open than to close (Evinger et al., 1991). The absence of visual information that cannot enter the eyes when we blink is called the *blackout*, which lasts 100–300 ms (Lawson, 1948a, 1948b; Lord & Wright, 1948). This duration varies across people (Slater-Hammel, 1953) and occurs for all blink types (Manning, Riggs, & Komenda, 1983; Volkmann, 1986; Volkmann, Riggs, & Moore, 1980). Why do we not perceive these blackouts?

2.0.2.1: Visual suppression during blinking

The blackouts are suppressed during the blink. In fact, visual information is suppressed during the blink. For example, flashes of light to the retina via a fiber-optic cable placed in participants' mouth are suppressed during the blink. In the experiment, participants were instructed to open their eyes, blink, or closed their eyes as directed by the experimenter. The experimenter then administered light flashes of varying luminance magnitudes. Participants verbally reported if they saw the flash. Results showed that participants had more difficulty detecting the flash when blinking than when their eyes were closed (Volkman, Riggs, Ellicott, & Moore, 1982). Luminance was suppressed during the blink which meant that visual suppression occurred when the observer blinked. This implied that we do not perceive the blackouts associated when blinking due to suppression. Otherwise, our visual world would become filled with periods of blackouts (Riggs, Volkman, & Moore, 1981; Volkman et al., 1982).

Some visual features that changes during blink suppression are undetected. For example, changes to luminance, but not color, is undetected during blinks (Burr, Morrone, & Ross, 1994; Ridder & Tomlinson, 1995). Changes to object positions in a natural scene at the start of a blink are also undetected, and are noticed in 40% of the attempts after the blink ended (O'Regan, Deubel, Clark, & Rensink, 2000). Visual transients in the cortex are also partially suppressed during the blink (Golan et al., 2016).

Volkman and colleagues (1980) speculated that blink suppression contributes to perceptual continuity since blinks cause large perturbations to vision but are often not perceived. The suppression induced by eye blinks minimizes the perception of blinking, resulting in a continuous experience of the visual world. Visual information is dampened as the blink occurs. Thus, we neither perceive the blackouts during each

blink, nor perceive the blink. More recent studies show evidence of this suppression. Specifically, visual cortex activity in epilepsy patients with brain implants show decreased visual activity during the blink (Golan et al., 2016). However, is our perception continuous simply because we are unaware of the disruption?

2.0.3: Change blindness in perceptual continuity

Perception could be continuous because we are unaware of changes. We do not think that an object has changed if we do not notice the change. We are blind to large changes in a visual scene (Simons & Levin, 1997). Observers may not readily detect obvious changes in the scene. For instance, it can take up to 30 seconds for observers to find the change when the original and alternate (i.e. scene with a change) scenes change every 300 ms (Huettel, Güzeldere, & McCarthy, 2001).

The failure to detect changes is not because of poor visual processing. Rather, it is due to attention. Changes are detected when attending to the changed area (Tse, 2004). Attention is more frequently directed to changes in the foreground than the background (Mazza, Turatto, & Umiltà, 2005). Large, but subtle, changes that do not catch attention are undetected. Changes remain undetected if unattended (Simons, Franconeri, & Reimer, 2000). The prefrontal and the parietal cortex involved with attention show enhanced activity when changes are detected as compared to undetected changes (Beck, Rees, Frith, & Lavie, 2001; Huettel et al., 2001). However, attending to a location does not guarantee change detection.

2.0.3.1: Awareness in change blindness and controversies

Awareness is also involved in change detection. Visual awareness is determined by recurring processes during perception. Recurring processes are the interactions between visual sensory information, feedforward signals from the eye, and feedback from higher areas at each level of visual processing (Lamme, 2003).

Awareness precedes change detection (Koivisto & Revonsuo, 2003). Merely fixating around the area of a change does not always improve change detection (Kuhn & Tatler, 2005; T. Smith, Lamont, & Henderson, 2012). We observe neural activity for the change before the observer reports the change and such activity is interpreted as awareness (Darriba, Pazo-Álvarez, Capilla, & Amenedo, 2012; Niedeggen, Wichmann, & Stoerig, 2001).

There are some controversies surrounding the notion that awareness precedes change detection. Fernandez-Duque and Thornton (2000) first showed that participants performed at above-chance level even if they reported unaware to the change. The researchers then introduced valid and invalid cues to the change detection task. Participants performed accurately when cues were valid, and participants were aware of the change. Yet, when participants were unaware of the change, they also performed significantly better at change detection regardless of the cue. Thus, Fernandez-Duque and Thornton indicated that awareness may not entirely explain change detection. There are debates surrounding whether attention and awareness is the same construct (Kentridge, Nijboer, & Heywood, 2008; Lamme, 2003). However, this is beyond the scope of the thesis. In the next section, we visit some explanations regarding the failure to detect changes.

2.0.3.2: Theories that explain why we are blind to change

There are several explanations why we are blind to changes in the environment. From a philosophical viewpoint, Dretske (2007) explained that the blindness was a “failure to notice (and, hence, know), not a failure to see” (pp. 216). He notes that the key assumption of change blindness that experimenters make, is that an observer is only aware of changes when the observer can tell the differences. Dretske argues that this assumption is false with the following example: An observer

is looking at seven people seated around a table. This observer scans the other people and looks away. While the observer looks away, a new person joined the group. There are now eight people, clearly visible, seated around the table. When the observer looks back, the observer does not notice the eighth person. This is typically defined as change blindness in psychological experiments. However, the observer was not blind to the eighth person since that person was clearly visible. Rather, the observer did not notice the eighth person. Dretske argued that what psychologists fail to distinguish is the difference between seeing (i.e. eight people seated around a table) and noticing (i.e. realizing there are eight people, instead of seven, seated around a table). Therefore, change blindness is not so much the ability to detect differences, but an issue in which an observer can see the change but not notice the change.

Change blindness could be explained by a lack of internal representations for undetected changes (Noë, 2005). Internal representation refers to a snapshot of the environment in which the visual system uses to reconstruct perception. We do not have a detailed representation of the visual environment. If we did, then change blindness would not occur as the visual system would reconstruct perfectly detailed representations of the visual environment. The lack of details in our internal representation of the visual world does not prevent us from experiencing details or having a perception of the physical world (Noë, Pessoa, & Thompson, 2000).

Change blindness could arise due to the constraints of our sensory system, in addition to the lack of internal representation of the change. According to O'Regan and Noë (2001), the conscious visual experience of an observer is based on how the observer moves his/her eyes to explore the world. This is regulated by *sensorimotor contingencies*, which are the rules and limitations of the sensory organs. These contingencies determine the information sensory organs collect. The observer controls

the sensory organ and is aware of the sensorimotor contingencies. Visual awareness arises as the observer rationalizes the information from the sensory organ and makes decisions on the information. Visual perception, then, becomes an act of exploring the visual world and comprehending information of the sensory contingencies. When the observer lacks data, nothing gets registered in perception. The following concrete example illustrates this theory: the eyes are constrained by oculomotor muscles which influences where we can look. One such constrain is that we cannot turn our eyes to look at the socket. We receive visual information based on what the eye can collect. As we explore the visual world via eye movements, we become aware of what we are seeing. In the case of change blindness, if we do not move our eyes to see the change, we do not have a representation of the change. Therefore, we do not perceive the change.

Those less fervent on the explanation of change blindness and internal representations argue that change blindness is simply the observer's shortcomings at comparing differences. In an experiment, Simons and colleagues (2002) tasked participants to observe scenes in a basketball match. The basketball was either abruptly removed, or unexpectedly switched to a brightly colored one, in one of the scenes. Later, the experimenters questioned the participants if they saw any strange occurrences regarding the scenes. Most participants did not spontaneously report the missing basketball or the brightly colored ball until they were asked questions about the nature of the ball. These results indicated that participants do have good memory (i.e. internal representation) of the scene, and that the failure to report the missing basketball until prompted was due to participants being bad at comparing scenes. Observers had good memory (representation) of a scene but could not identify the change because the change have yet to overwrite memory. Memory of the scene was

overwritten when participants were prompted with questions concerning the missing basketball. Alternatively, being bad at comparisons in change blindness could be due to the limited cognitive abilities to pick specific information in a scene flooded by an expansive visual memory (Block, 2011).

In summary, the failure to detect changes could occur because observers failed to notice the change, lacked representations for the change, were limited by the constraints of the sensory systems, or were simply bad at comparing changes. In the next section, we discuss change detection during endogenously induced disruptions (i.e. blinking) and how blink adaptation could be a functioning unit for temporal stability.

2.0.4: Position change detection and blink adaptation

If temporal stability is the lack of change detection which also ignores endogenous disruptions from the blink, what happens to an observer's fixation if the object changes position during the blink? Positional changes of an object during blinks are difficult to detect (Maus et al., 2017). In experiments involving solely spontaneous blinks, observers fixated a white dot. Participants were asked to fixate the dot throughout the experiment. The dot was displaced by 0.5° or 1° rightward during each blink. However, participants were not briefed about the displacement during the blink. Participants could not see the displacement happening. Results revealed that the gaze position gradually adapted to the displaced dot position after many trials, even when participants were unaware of the displacement. This phenomenon was then termed *Blink Adaptation*, in which the gaze position landed closer to the displaced dot position after each blink. After adaptation, when the dot remained stationary, the gaze position landed ahead of the dot as if the dot was displaced. Gaze compensated on average for about 70% of the displacement after the blink and the effect was

extinguished quickly. Could blink adaptation be a functioning unit for temporal stability?

2.0.5: Investigating blink adaptation

Less is known about the extent of blink adaptation because it is recently discovered. Does blink adaptation occur for other displacement directions? If blink adaptation does not occur in other displacement directions, gaze is not corrected towards the displaced target after blinking. The discrepancies before and after blinking becomes apparent and observers would effectively detect the difference, forfeiting continuity. Additionally, is there blink adaptation when observers are aware of the displacement? There should be no adaptation when observers are aware of the displacement because observers would remain fixated at the original position instead of the displaced position. This translates to a break in the position continuity of an object, since the observer is now aware, after blinking, that the object has displaced.

Anisotropies in saccades could be present in blink-related eye movements. Saccades and saccadic velocities differ depending on the trajectory. Saccade velocity and position, along the horizontal plane, of the abducting (temporally moving) eye is greater than the adducting (nasally moving) eye (Collewyn, Erkelens, & Steinman, 1988a). Saccade amplitudes, along the vertical axis, tend to undershoot upward targets and overshoot downward targets (Collewyn, Erkelens, & Steinman, 1988b). These anisotropies in saccadic movements may also apply to blink-related eye movements during blink adaptation of other displacement directions.

Can other kinds of blinks elicit adaptation? Different blinks have specific physiological characteristics (Kaneko & Sakamoto, 1999) but the blinking motion is thought to be controlled by the same pre-motor neuron (Korošec, Zidar, Reits, Evinger, & Vanderwerf, 2006). Spontaneous blinks are thought to be controlled by

basal ganglia activity (Ponder & Kennedy, 1927). The basal ganglia may also trigger reflexive blinks by inhibiting the brainstem, although the exact circuitry is not well-understood (Valls-Sole, 2012). Maus et al. (2017) found adaptation for spontaneous blinks but did not test for other blink types. If reflexive blinks cannot reproduce the adaptation, then it is possible the adaptation is part of a unique component found in the spontaneous blink circuitry but not the reflexive blink circuitry.

2.1.0: Experiment 2.1 and 2.2 investigates blink adaptation using voluntary and reflexive blinks

Blink adaptation shifts gaze closer to a displaced target during the blink. The target does not appear displaced after the blink because the gaze-to-target distance is minimized. We would expect the same effect for targets displaced in different directions if blink adaptation is a behavior that preserves perceptual continuity for object positions. In Experiment 2.1, we tested horizontal and vertical dot displacements separately. We hypothesized that blink adaptation was evident for horizontal and vertical displacements. In Experiment 2.2, we investigated whether blink adaptation was also evident in reflexive blinks by eliciting air-puffs. If adaptation did not occur for reflexive blinks, it would suggest that the blink adaptation behavior involved a unique component in the spontaneous blink circuitry.

Methods

2.1.1: Participants

Maus et al. (2017) recruited a total of 13 participants for different experiments. Some participants also completed multiple experiments. We initially recruited six participants based on their experiment 1. However, we had to discard data from participants who wore contacts or glasses because the data was noisy. At the end of Experiment 2.1, we recruited a total of 21 participants ($M = 23.19$ years old, $SD =$

2.18, 14 females) from Nanyang Technological University. Of which, data from eight participants with glasses/contacts were discarded ($N = 13$, $M = 23.38$ years old, $SD = 2.63$, 10 females).

We did not expect that frequent blinking would cause the glasses/contacts to change positions, thereby distorting the data. The facial muscles move when participants blink. This causes the glasses to slide lower down the nose-ridge. This affected the eye-tracker's infra-red (IR) sensor as the IR rays were sometimes reflected away from the camera during recording. As a result, eye tracking data was affected. We did not know the instance the glasses/contacts changed position during recording. Therefore, we did not perform re-calibration. We circumvented this problem by recruiting participants who did not wear glasses/contacts in Experiment 2.2.

For Experiment 2.2, we recruited participants who did not require glasses or contact lenses ($N = 13$, $M = 26.62$ years old, $SD = 3.10$, 3 females). Data from two participants were discarded from Experiment 2.2 ($N = 11$, $M = 26.27$ years old, $SD = 3.20$, 3 females). This was because the data were noisy or had fewer than 50 analyzable trials.

All participants, except for one, were naïve to the purpose of the experiment. Participants had normal or corrected-to-normal visual acuity and gave consent prior to the start of the experiment. Upon completion, participants were either rewarded with course credits or up to \$10/hr. The experiment was approved by Nanyang Technological University's institutional review board (IRB).

2.1.2: Stimulus and apparatus

The experiment was programmed on MATLAB (Mathworks Inc., Natick, MA, USA) and Psychtoolbox-3 (Kleiner et al., 2007). Visual stimuli were presented on a 20" Sun Microsystems CRT monitor at a resolution of 1152 x 864 and refresh

rate of 100 Hz. A chin rest was positioned 75 cm away from the monitor. The horizontal and vertical gaze coordinates and pupil area were tracked using an Eyelink 1000+ eye tracker (SR Research, Ottawa, Ontario, Canada). Tracking was monocular (right eye) but viewing was binocular. Blinks were detected online. Blinks were defined as the period where the eyelid completely closes the eye (pupil area = 0).

The stimulus was a white dot (diameter = 0.2°) displayed on a black background (black = 0.75 cd/m^2 , white = 132 cd/m^2) in both experiments (Figure 27). We confined the stimulus to an area $15.79^\circ \times 11.84^\circ$ about the center of the screen. The dot was displaced by 0.25° in one of four directions (left, right, up, or down) whenever a blink was detected. Displacements never occurred for two or more directions within a condition. The dot was randomly assigned to a new location within the confined area after 2–6 blinks to prevent the dot from moving off screen.

Figure 2.1.1. Trial sequence for Experiment 2.1 and 2.2. The dot and displacement step are enlarged for illustration. Each blink was considered a trial. The dot was displaced by 0.25° in one of four directions during a spontaneous/voluntary blink (Experiment 2.1), or a reflexive blink in response to an air-puff (Experiment 2.2). The dot was always displaced in the same direction throughout one condition. In this example, the dot was displaced rightward. The dot was displaced during adaptation and top-up trials.

2.1.3: Procedure for both experiments

We tested voluntary/spontaneous blinks in Experiment 2.1 and reflexive blinks in Experiment 2.2. Participants gave consent before the experiment. They were instructed that the task was to look at the stimulus and that the stimulus would relocate to a new location frequently. After which, we calibrated the eye tracker using the 9-point calibration and validation procedure on the right eye. We then reminded participants to fixate the stimulus throughout the experiment. When ready, participants began the experiment by pressing a button on the keyboard.

Each blink was considered a trial. There were 105 trials per run. The dot was displaced in a single direction in each run. Trials within a run were distributed into adaptation, post-adaptation, and top-up. There were 40 trials in adaptation, 5 trials in post-adaptation, and 15 trials top-up. The sequence of a run was as follows: 40 adapt, three cycles of 5 post-adapt and 15 top-ups, and a final 5 post-adapt. The dot was displaced in a different direction per run.

In each experiment, participants completed two runs of the same orthogonal displacement directions (e.g. up & left, up & right, down & left, or down & right). Orthogonal direction pairs were randomly assigned. The first direction within the orthogonal pairs was randomized to eliminate order effects. Opposite directions were not tested to prevent carry-over effects. At the end of each experiment, we asked participants if they noticed the displacement during the blinks. In Experiment 2.1, 10 participants (77%) reported being unaware of the displacement, whereas in Experiment 2.2, 10 participants (91%) said they were unaware of the displacement.

2.1.3.1: Experiment 2.2 air puff details

In Experiment 2.2, reflexive blinks were elicited by air puffs. Air puffs were administered electronically to the left eye. An Arduino Micro board operated a valve

connected to the PC. The valve then released the air puffs. When the valve opens, compressed air exited a compressor tank at 10–20 psi (Bolbecker et al., 2009; N. J. Gandhi & Bonadonna, 2005). Each 50 ms puff was delivered along a plastic tube positioned ~1 cm away from the eye. The tube was directed to the skin surface surrounding the left eyebrow and eyelid. There was an additional pressure regulator which adjusted the output air pressure to a comfortable level. Based on feedback from a pilot experiment, participants reported having the least number of adverse reactions (such as dry eyes) when using this location to trigger the reflexive blinks. Occasionally, a manual puff was triggered via a keypress by the experimenter, when participants did not reliably blink following air puffs.

2.1.3.2: Experiment 2.2 air puff training

All participants in Experiment 2.2. underwent air puff training trials before the experiment. The training goal was to habituate participants to the air puff. Participants who could not habituate to the air puffs did not participate in the experiment. We first measured the resting blink rate for participants before training began. Participants observed a black/blank screen for three minutes while relaxed. We then computed blink intervals to derive a blink-interval histogram. We fitted a gamma distribution to the histogram to generate random inter-blink intervals (as in Experiment 2 in Maus et al., 2017). The intervals were limited to between 1.5–6 s for administering the air puffs. The two reasons for the restriction were: 1) to reduce the runtime of the reflexive blinks condition such that participants made as little spontaneous blinks as possible while completing the experiment mostly with reflexive blinks, and 2) to avoid participants not blinking reflexively to a second air puff after too short intervals (i.e. air puffs at < 1.5 s intervals).

Participants then accustomed to the air puffs. The goal of habituation was to blink only once after each puff. Without habituation, participants would blink uncontrollably after a puff. Training lasted approximately 35 mins inclusive of breaks. Training sequence were as follows: (i) a puff every three seconds for 90 s, (ii) a puff every three seconds for three minutes, and (iii) a puff randomly between 1.5–6 s based on the gamma distribution. We manually triggered an air puff several seconds later with the same intensity and puff duration via keypress whenever participants did not react to the puff. The experiment began immediately after training.

2.1.4.1: Analysis for gaze calculations

Post-blink gaze positions were analyzed offline using MATLAB (Mathworks Inc., Natick, MA, USA). Statistical analyses were conducted on SPSS version 20.0 (IBM Corp., Armonk, N.Y., USA). The procedures for conducting offline analysis were adapted from the original study (Maus et al., 2017). The details were as follows: eye tracker sample where pupil area = 0 indicated blink start. The average gaze position -200 ms to -100 ms before blink start was the pre-blink gaze position. We calculated the pre-blink gaze interval variance. Blink end was defined as the timepoint in which the pupil area exceeded 80% of the pupil area before the blink. We then ran a 10 ms sliding window beginning from blink end and calculated the variance within this window. Stable gaze position after the blink was identified as the first available sample in which the variance of the sliding window fell below 1.5 times the pre-blink gaze interval variance. From the stable gaze position, we computed the post-blink gaze position by averaging up to 100 ms from the start of the stable gaze position (or until the first saccadic eye movement after the blink, whichever was shorter). Post-blink gaze position was subtracted from pre-blink gaze position. Pre-blink gaze position was

defined as 0° . We manually inspected post-blink gaze positions to ensure no false detections.

Outliers (mean post-blink gaze position $\pm 1.37^\circ$ from the dot) from each participant were removed from the data. This ensured that we only analyzed data where participants were fixating. 61 trials (.03%) from Experiment 2.1 and 81 trials (.05%) from Experiment 2.2 were removed in total. The average blink duration for Experiment 2.1 was 208.85 ms (SD = 101.60) and the average blink duration for Experiment 2.2 was 165.59 ms (SD = 92.24).

2.1.4.2: Analysis for time-course

Data was time-locked to the blink number in each run for all participants. For instance, blink #1 was the first blink across all participants in the corresponding displacement direction and experiment. The data was transformed such that positive values indicated a change in the adaptation/displacement direction. We calculated the average post-blink gaze position for early adaptation blinks (blinks 1–10) and late adaptation blinks (blinks 31–40). From here, we refer to early adaptation blinks and late adaptation blinks as early and late blinks.

A time-course analysis illustrated the development of post-blink gaze positions over the experiment. The time-course provides an important information in determining systematic biases in post-blink gaze positions. We used a one-way ANOVA to evaluate post-blink gaze across directions in the early phases of the experiment. The justification for comparing the early phases was because blink adaptation takes time to develop. There were no systematic biases if post-blink gaze positions across directions did not differ from each other.

2.1.4.3: Analysis for blink adaptation

We investigated whether blink adaptation occurred by comparing post-blink gaze positions between early and late adaptation blinks. We conducted a one-way repeated-measures ANOVA to assess whether the early blinks differed from late blinks. The between-group variable was directions (i.e. up, down, left, and right) and the within-group variable was experiment phase (early and late blinks). We used one-samples *t*-tests to assess whether early and late blinks differed from zero for each direction.

Post-adapt data for each participant were computed by pooling all post-adapt trials in each displacement direction (i.e. blink 41-45, 61-65, 81-85, and 101-105). We then conducted a 4x3 ANOVA to determine if there were differences between post-blink gaze positions across the four directions and experiment phase (early, late, and post-adapt).

We collapsed the data across horizontal and vertical directions to increase statistical power. Left and right displacements were recoded as horizontal displacements. Up and down displacements were recoded as vertical displacements. We calculated the average early, late, and post-adapt blink positions for horizontal and vertical displacements. We then conducted a 2x3 ANOVA to investigate blink adaptation across horizontal and vertical displacements. The between-subjects factor was directions (i.e. horizontal/vertical) and the within-subjects factor was experiment phase.

We compared gaze positions across experiments to test blink adaptation between voluntary and reflexive eye blinks. Data was pooled across all directions per experiment. We then ran a 2x3 ANOVA where the between-subjects factor was blink

types and the within-subjects variable was experimental phase. The alpha value across all analyses was $p = .05$.

Results

2.1.5.1: Experiment 2.1

In Experiment 2.1, we evaluated whether early blinks were significantly different from late blinks across directions. The time-course analysis (Figure 2.1.2) did not reveal systematic biases between displacement directions in the early phase of the experiment, $F(3, 17) = .09, p = .96$.

Figure 2.1.2. Time-course analysis for Experiment 2.1. Arrows depict the direction of the dot displacement: a) upward, b) downward, c) leftward, & d) rightward. Dot was displaced by 0.25° . Error bars represent SEM. Positive values in the figure reflect gaze position in the same direction as the displaced dot. The dot was not displaced during post-adaptation.

The next analysis compared post-blink gaze positions across different experiment phases (Figure 2.1.3). One-way repeated measures ANOVA revealed no significant differences in experiment phase across directions, $F(3, 14) = 0.87, p = .48$.

We compared whether early and late blinks differed from zero. Early blinks were not statistically different from zero across directions: upward, $t(5) = -2.22$, $SD = 8.68$, $p = .08$, downward, $t(3) = -1.06$, $SD = 35.90$, $p = .37$, leftward, $t(3) = -2.58$, $SD = 2.54$, $p = .08$, and rightward, $t(3) = 2.83$, $SD = 4.52$, $p = .07$. Late blinks were substantially different from zero for leftward displacements, $t(3) = -5.54$, $SD = 2.68$, $p = .012$. There were no differences for the remaining directions: upward, $t(5) = -2.18$, $SD = 11.01$, $p = .08$, downward, $t(3) = 1.90$, $SD = 8.90$, $p = .15$, and rightward, $t(3) = 2.90$, $SD = 8.63$, $p = .06$.

Figure 2.1.3. Post-blink gaze position for early, late, and post-adapt blinks. Symbols indicate individual data. Gray dotted line illustrates where the displaced dot was after the blink. Each color indicate the displacement direction. Error bars denote standard error of mean (SEM).

Next, we investigated adaptation aftereffects by comparing post-adapt blinks to early and late blinks across direction. There was no statistical main effects for directions, $F(3, 44) = 1.40$, $p = .25$, no significant main effects for experiment phase, $F(2, 44) = 0.68$, $p = .51$, and the interaction effect was insignificant, $F(6, 44) = 0.82$, p

= .56. We pooled the data and evaluated the post-blink gaze position between horizontal (left and right) and vertical (up and down) directions, and experiment phase. Again, there was no statistical main effect for directions, $F(1, 50) = 0.20$, $p = .66$, and for experiment phase, $F(2, 50) = 0.81$, $p = .45$. The interaction term was not significant, $F(2, 50) = 1.08$, $p = .35$.

In summary, the data from voluntary blinks late blinks for leftward displacements were significantly different from zero. However, repeated measures ANOVA did not indicate evidence of blink adaptation across directions. There were no differences for horizontal and vertical directions.

2.1.5.2: Experiment 2.2

In Experiment 2.2, we tested whether adaptation occurred in reflexive blinks by comparing between early and late blinks across directions. The time-course analysis (Figure 2.1.4) did not reveal systematic biases between displacement directions in the early phase of the experiment, $F(3, 15) = .41$, $p = .75$.

Figure 2.1.4. Time-course analysis for Experiment 2.2.

In the next analysis, we compared post-blink gaze positions across various experiment phases (Figure 2.1.5). Repeated measures ANOVA did not show any differences between directions and experiment phase, $F(3, 12) = 2.00$, $p = .17$. We then determined if early and late blinks differed from zero. There were no statistical differences between early blinks and zero across directions: upward, $t(3) = -1.37$, $SD = 20.87$, $p = .26$, downward, $t(3) = -2.94$, $SD = 3.09$, $p = .06$, leftward, $t(3) = -1.27$, $SD = 5.84$, $p = .29$, and rightward, $t(3) = 1.77$, $SD = 5.54$, $p = .18$. Late blinks were substantially different from zero for leftward displacements, $t(3) = -14.26$, $SD = 1.09$, $p = 7.47 \times 10^{-4}$. There were no differences for the other directions: upward, $t(3) = -1.46$, $SD = 25.77$, $p = .24$, downward, $t(3) = -.78$, $SD = 12.75$, $p = .49$, and rightward, $t(3) = 3.15$, $SD = 6.00$, $p = .05$.

Figure 2.1.5. Post-blink gaze position for early, late, and post-adapt blinks. Symbols indicate individual data. Gray dotted line illustrates where the displaced dot was after the blink. Each color indicate the displacement direction. Error bars denote standard error of mean (SEM).

We then compared post-adapt blinks to early and late blinks across directions. There was no substantial main effects for directions, $F(3, 40) = 2.29$, $p = .09$, nor for

experiment phase, $F(2, 40) = 1.00, p = .38$. The interaction term was insignificant, $F(6, 40) = 0.88, p = .52$. We pooled the data across horizontal and vertical directions to test for adaptation across directions. There was no significant main effect for direction, $F(1, 46) = 0.21, p = .65$, and no differences for experiment phase, $F(2, 46) = 0.93, p = .40$. The interaction effect was not different, $F(2, 46) = 1.07, p = .35$. We tested if voluntary blinks differed from reflexive blinks. There was a significant main effect between voluntary and reflexive blinks, $F(1, 74) = 4.03, p = .048$, but no differences between experiment phase, $F(2, 74) = 2.53, p = .09$. The interaction effect was not significant, $F(2, 74) = .14, p = .87$.

In summary, results across both experiments indicated that late blinks for leftward displacements were significantly different from zero. However, repeated measures ANOVA did not indicate evidence of blink adaptation across directions. There were no statistical differences for horizontal and vertical directions. Gaze position for voluntary blinks (Experiment 2.1) was significantly different from reflexive blinks (Experiment 2.2).

Discussion

2.1.6: Not enough evidence to suggest blink adaptation

Blink adaptation brings the gaze closer to a displaced target during the blink, when the target is displaced rightward. However, less is known if the effect also applied to other displacement directions. We investigated the extent of blink adaptation by displacing targets in one of four directions (Experiment 2.1). We also tested if reflexive blinks elicited adaptation (Experiment 2.2).

In Experiments 2.1 and 2.2, there were not enough evidence to suggest blink adaptation because of the lack of baseline comparisons. We compared post-blink positions between voluntary and reflexive blinks. We found a statistical main effect

between the two blink types. This signified that voluntary and reflexive blinks were different. However, we did not find any differences for directions between blink types.

2.1.6.1: The two significant results

There were two analyses which achieved significance. In Experiment 2.1, we found substantial differences between late blinks and zero. We also found differences between voluntary and reflexive blinks. It is tempting to suggest blink adaptation in Experiment 2.1, and that voluntary and reflexive blinks are different. However, we exercised caution in drawing these conclusions because of the flaws addressed in 2.1.6.2.

Subtracting gaze positions before and after the blink cannot be zero. According to the literature, eye movement traces reveal small differences in gaze positions before and after the blink (Collewijn, Erkelens, & Steinman, 1995; Riggs et al., 1987). In our experiments, we compared post-blink gaze positions to a static value 0. This value does not accurately reflect the differences between the gaze positions before and after blinking. Since gaze positions before and after blinking are not exact, it would be important to measure this difference, before making other comparisons. Therefore, we could argue that Experiment 2.1 exhibited blink adaptation for leftward displacements, but this argument lacks a good comparison about how the gaze changes when no adaptation occurred.

Voluntary and reflexive blinks could recruit different blink-related circuitry, thus, producing different gaze behaviors after the blink. However, it is difficult to confirm this claim with our current data. We could not rule out the contributions from group effects because two groups of participants completed different experiments. If we replicated this in a within-subjects design experiment, it would greatly support the argument that voluntary and reflexive blinks tap onto different blink circuitry. In the

next section, we addressed the flaws to improve the experiment design and analysis to better support our claims.

2.1.6.2: The lack of a baseline

The results were not interpretable because of the lack of a baseline. Maus et al. (2017) provided clear evidence for blink adaptation by comparing post-blink gaze positions and the baseline. The dot was not displaced during the blink for baseline trials. When the dot was displaced by 0.5° , the post-blink gaze for early blinks were not significantly different from baseline, but the late blinks were significantly different from the baseline. This showed that the different post-blink gaze positions were attributed to adaptation instead of some unexplained biases. Thus, in the following experiments, we collected post-blink baselines at the start of the experiment.

2.2.0: Motivation for experiments 2.3 and 2.4

Signal-to-noise could be a concern for the lack of results in the experiments. It can be difficult to isolate a signal in very noisy data. In the original study (Maus et al., 2017), the dot was displaced by 0.5° and 1.0° . Displacement sizes of 0.71° were also used in a separate blink-related experiment (Higgins, Irwin, Wang, & Thomas, 2009). To increase signal-to-noise ratio, we opted to displace the dot by 0.7° in the following experiments. This magnitude is approximately between those used in the original study which further complements the current literature.

Besides testing for blink adaptation in different displacement directions, we do not know if adaptation occurs concurrently in both eyes. In the original study, Maus and colleagues (2017) only measured the right eye. According to Hering's Law, both the left and right eyes are equally yoked (Hering, 1977). Agonistic and antagonistic extraocular muscles ensure that uniocular movements of one eye approximate those of the other eye. The yoked nature of both eyes is clear when making saccades; both eyes

move in the same direction towards a target. However, eye movements are drastically different during a blink. When the blink begins, both eyes turn nasally inward while moving downwards. The eyes then rotate temporally outwards while moving upwards to the previous position (Collewyn et al., 1985; Rottach, Das, Wohlgenuth, Zivotofsky, & Leigh, 1998). Importantly, the eye is already returning to an approximate previous position before the lid closes the eye (Riggs et al., 1987). Blink-related eye movements help to reset torsional eye movements (Khazali, Pomper, Smilgin, Bunjes, & Thier, 2016) and correct for fixational errors (Khazali, Pomper, & Thier, 2017). Does blink adaptation occur currently in both eyes because the eyes are yoked? Since both eyes experience asymmetrical movements during a blink, we might expect anisotropies in each eye in blink adaptation.

2.2.0.1: Experiment 2.3 tests larger displacements, and experiment 2.4 tests for binocular adaptation

The following experiments were published in Lau and Maus (2019a). Experiments 2.3 and 2.4 included baseline trials and increased displacement magnitude ensure good signal-to-noise ratio when measuring post-blink gaze position. In Experiment 2.3, we recorded the right eye, while in Experiment 2.4, we recorded both eyes. Viewing was binocular in both experiments. The goal of Experiment 2.3 was to test whether a larger displacement magnitude, 0.7° , could elicit blink adaptation, and if reflexive blinks triggered by air-puffs would exhibit adaptation. All participants completed voluntary/spontaneous and reflexive blink conditions. We compared adaptation magnitudes between the different blink types within the same participants. We hypothesized that blink adaptation was controlled by a general circuitry which produces both blinks. Adaptation should be present in both reflexive and voluntary/spontaneous blinks. However, if blink adaptation was observed in only

one blink type, this would suggest that adaptation is dependent on the circuitry specific to this blink type.

In Experiment 2.4, we examined whether blink adaptation differed between both eyes by recording binocular data. Blink-related eye movements are asymmetrical between each eye, whereas other eye movements are generally yoked. If blink adaptation was caused by a change in blink-related movements, then we expect anisotropies between the two eyes. However, if adaptation was not caused by altered blink-related movements, then we would see the same amount of adaptation in both eyes.

Methods

2.2.1: Participants

Participants were recruited from Nanyang Technological University. 20 participants ($M = 21.50$ years old, $SD = 2.60$, 15 females) were recruited for Experiment 2.3. All participants, except for one, were naïve to the purpose of the experiment. We avoided recruiting participants with corrective contact lenses to not exacerbate potential dry eye problems in lens wearers with the application of air puffs. A new group of 12 participants ($M = 21.25$ years old, $SD = 1.48$, 9 females) were recruited for Experiment 2.4. Seven participants had normal visual acuity, five wore corrective contact lenses. All participants gave informed consent prior to the start of the experiment. Upon completion, participants were either rewarded with course credits or up to S\$10/hr. The experiment was approved by Nanyang Technological University's institutional review board (IRB).

2.2.2: Stimulus and Apparatus

The stimulus and apparatus for Experiment 2.3 and 2.4 was identical to Experiment 2.1 and 2.2 (see 2.1.2). The dot was displaced in one of four directions

(left, right, up, or down) by 0.7° whenever a blink was detected during the experiment (Figure 2.2.1). Participants were aware that frequent blinking was necessary to complete the experiment. Participants were randomly assigned to a pair of displacement directions: Up & Right ($N = 10$, $M = 21.60$ years old, $SD = 3.07$, 6 females) or Down & Left ($N = 10$, $M = 21.40$ years old, $SD = 2.01$, 9 females). Opposing directions were not tested to prevent carry-over effects.

Figure 2.2.1. Trial sequence for Experiment 2.3. The dot and displacement step are enlarged for illustration. Each blink was considered a trial. The dot is displaced by 0.7° in one of four directions during a spontaneous/voluntary blink, or a reflexive blink in response to an air-puff in each block. In this example, the dot was displaced rightward. The dot was displaced during adaptation and top-up trials. The trial sequence for Experiment 2.4 is identical, but both eyes were recorded, and no air puffs were used.

For Experiment 2.3, participants made voluntary/spontaneous blinks in one condition, and reflexive blinks in the other. We recorded eye movements for the right eye. Participants were encouraged to blink once every 3–4 s in the voluntary/spontaneous blinks condition. Most blinks in this condition might more accurately be characterized as voluntary eye blinks. However, spontaneous blinks might also have occurred during the run. The dot was displaced for both spontaneous and voluntary blinks. Therefore, we do not strictly distinguish between spontaneous

and voluntary blinks. For Experiment 2.4, participants made only voluntary/spontaneous blinks, and the eye tracker recorded movements of both eyes.

The first ten blinks of each experiment were called the baseline. During the baseline, the dot appears only at screen center. Participants fixated the dot and blinked. The dot was not displaced during the blink. The purpose of the baseline was to determine where the participants were looking after the blink for a stationary dot. This was also used to identify whether participants were biased to look elsewhere after blinking.

2.2.3.1: Procedure – experiment 2.3

Participants gave consent before beginning the experiment. They were told the task was to look at the dot on the monitor throughout the experiment. They were also briefed that the dot would move to a new location frequently (referring to the obvious location changes in-between blinks) but were not told about the position changes during blinks.

There were two conditions: spontaneous/voluntary blinks condition, and reflexive blinks condition. Conditions were randomized and participants completed each condition on separate visits. Participants completed resting-state measurements and training before commencing the reflexive blink condition (see Experiment 2.2). During the reflexive blink condition, the dot was never displaced for voluntary/spontaneous blinks. Only blinks occurring up to 150 ms after the air puff were considered reflexive blinks. Otherwise, the blink was treated as a voluntary/spontaneous blink. When participants did not react to the air puff, we manually triggered the air puff several seconds later using keypress with the same intensity and puff duration, which tended to lead to a reflexive blink in most cases.

The procedure for the voluntary/spontaneous blink condition was the same as in Experiment 2.1.

Each blink was considered a trial. There were 115 trials per run. The dot was displaced in a single direction in each run. Participants completed two runs of orthogonal displacement directions (i.e. up & right, or down & left) per condition, for a total of four runs. The pair of orthogonal directions were randomly assigned, and participants started with a random direction. The displacement directions for voluntary and reflexive blink conditions were the same within each participant. Each run for Experiment 2.3 consisted of the following components: 10 baseline trials, 40 adaptation trials, and three sets of 5 post-adaptation trials and 15 top-up trials each, and a final set of 5 post-adaptation trials, for a total of 115 trials.

2.2.3.2: Procedure – experiment 2.4

Participants completed four runs, one for each of the four directions. Directions were randomized. Instructions regarding the task and the frequent re-location of the dot between blinks were the same as Experiment 2.3. Participants were not told about the position changes during blinks.

We only tested voluntary/spontaneous blinks for Experiment 2.4. The procedure was the same as Experiment 2.1. Each run for Experiment 4 consisted of: 10 baseline trials, 60 adaptation trials and two sets of 5 post-adaptation and 15 top-up trials each, and a final set of 5 post-adaptation trials, for a total of 115 trials. The larger number of adaptation trials for Experiment 2.2 was to elicit stronger adaptation and allow for longer saturation of adaptation.

At the end of each experiment, we asked our participants whether they noticed the dot was displaced during blinks. 17 (85%) participants in Experiment 2.3 and 6

(50%) participants in Experiment 2.4 reported being unaware of the dot displacements during blinks.

2.2.4.1: Analysis – gaze calculation

Gaze position analysis were conducted on MATLAB (Mathworks Inc., Nattick, MA, USA), and statistical analyses were conducted on SPSS version 20.0 (IBM Corp., Armonk, N.Y., USA). The start of the blink was defined as the first eye tracker sample where no pupil area was detected (area = 0). The average horizontal and vertical gaze positions -200 ms to -100 ms before each detected blink (pre-blink gaze) were defined as 0°. The variance of this window was computed. Blink end was identified as pupil area exceeding 80% of the pre-blink gaze area after the blink started.

Tracker noise produces unstable estimates of gaze position immediately after a blink. The remedy for this is to look for stable gaze positions. We identified the first stable gaze position after the blink, when the standard deviation of gaze position values within a 10 ms-sliding window fell below 1.5 times the pre-blink gaze variance. The gaze position after the blink was computed by averaging gaze positions in a window from the start of the stable gaze position lasting 100 ms, or until the first saccadic eye movement after the blink, whichever was earlier. Gaze positions after the blink were manually inspected to ensure there were no false detections of saccades.

2.2.4.2: Analysis for time-course

Data was time-locked to the blink number in each run for all participants. For instance, blink #1 was the first blink across all participants in the corresponding displacement direction and experiment. The data was transformed such that positive values indicated a change in the adaptation/displacement direction. A time-course analysis was then conducted for Experiment 2.3 and 2.4. This analysis visualized the

development of post-blink gaze positions across the experiment. We used a one-way ANOVA to evaluate post-blink gaze across directions in the baseline. The baseline establishes neutral post-blink gaze positions when participants fixated on a stationary dot. There were no systematic biases if post-blink gaze positions across directions did not differ from each other in the baseline. The time-course plots for Experiment 2.4 were not visualized to reduce visual clutter. Instead, the analysis from the ANOVA was reported.

2.2.4.3: Analysis for single trial data in one participant

We calculated the post-blink gaze position by subtracting the gaze position after the blink from the pre-blink gaze position. Single-trial data of one participant from Experiment 2.3 was visualized to demonstrate how the pre-blink gaze and gaze position after the blink were derived from the analysis (Figure 2.2.2). This participant completed upward and rightward displacements in both voluntary (Figure 2.2.2a–d) and reflexive (Figure 2.2.2e–h) conditions. Reflexive blinks were quantified by blink duration < 100 ms. The latency between the puff and blink onset must also be < 150 ms. This interval was derived from a pilot experiment. Outliers were discarded when the mean post-blink gaze position exceeded $\geq 2^\circ$ about the dot position. This ensured that the post-blink gaze positions did not reflect trials where participants were not looking at the dot.

2.2.4.4: Analysis for blink adaptation

To investigate blink adaptation, we compared post-blink gaze positions against the phases in a run. For example, we compared the early adaptation blinks (blinks 11–20, the first 10 blinks with displacements), the late adaptation blinks (the last 10 blinks of the adaptation trials, e.g. blinks 41–50 in Experiment 2.3), and the combined post-

adaptation blinks (e.g. blinks 51–55, 71–75, etc. in Experiment 2.3; 20 post-adaptation trials in total from each experiment) to the baseline (blinks 1–10).

Figure 2.2.2. Time courses of gaze positions across single blinks (thin blue lines) and means for the whole experiment (thick, dark blue lines) from one participant in Experiment 3. This participant completed the upward (a, b, e, f) and rightward (c, d, g, h) displacements in voluntary (a-d) and reflexive (e-h) blink conditions. Only blinks from the baseline and late adaptation phases are shown. Up and leftward are plotted down on the abscissa. Pupil area (normalized) is plotted in red.

We conducted 4x4 ANOVAs to determine whether post-blink gaze in each direction differed across experimental phases for both experiments. The between-group variable was directions (i.e., up, down, left, and right), and the within-group variables were the phases (i.e. baseline, early, late, and post blinks). We used the Greenhouse-Geisser correction for all within-subjects analysis if Mauchly's test of sphericity was violated (Mauchly, 1940). Post-hoc analyses were performed using Bonferroni-corrected α on significant group differences.

In Experiment 2.3, we ran a repeated-measures ANOVA to evaluate if the post-blink gaze positions across experimental phase differed between blink types (voluntary vs. reflexive) in each participant. In Experiment 2.4, we performed a repeated-measures ANOVA to compare if adaptation magnitudes differed between each eye in the same participant. We ran a planned comparison paired t -tests to evaluate whether the phases contrasted from the baseline in each direction between blink types (Experiment 2.3), and between each eye (Experiment 2.4). The t -tests were significant if the p -value fell below the Bonferroni-corrected α of $.05/3 = .017$. We further calculated the adaptation gains for each direction by dividing the average gaze magnitude of the late blinks by the displacement magnitude of the dot (0.7°).

Results

2.2.5.1: Experiment 2.3

In the voluntary blink condition, the baseline phase showed no change of post-blink gaze from the pre-blink gaze, as expected (Figure 2.2.3 and 2.2.4). From the time-course analysis, one-way ANOVAs did not indicate differences in the baseline across directions for spontaneously/voluntary, $F(3, 36) = 1.40$, $p = .26$, and for reflexive, $F(3, 36) = .49$, $p = .69$, blinks. Introducing the fixation step during a blink, however, introduced positive biases in the post-blink gaze position towards the new

fixation position, moderately in the early adaptation phase, and more prominently in the later adaptation phase (Figure 2.2.5a). This bias persisted after the adaptation phase.

Experimental phases were significantly different within each direction, $F(3, 144) = 9.71, p = 7.06 \times 10^{-6}, \eta_p^2 = .20$ (Figure 2.2.5a). We conducted a planned comparison t -test to evaluate blink adaptation for each direction. Blink adaptation was observed if there were significant differences between late blinks and baseline blinks using Bonferroni-corrected $\alpha = .017$. Results exhibited blink adaptation across all directions; Upward: $t(9) = -3.70, SD = .28, p = .005, \text{Gain} = 21.01\%$, Downward: $t(9) = -6.44, SD = .31, p = .0001, \text{Gain} = 122.94\%$, Leftward: $t(9) = -3.07, SD = .29, p = .013, \text{Gain} = 28.85\%$ and Rightward: $t(9) = -8.03, SD = .19, p = 2.16 \times 10^{-5}, \text{Gain} = 82.96\%$.

We found significant differences in the post-blink gaze positions across the four directions, $F(3, 144) = 8.17, p = 4.66 \times 10^{-5}, \eta_p^2 = .017$. Post-hoc tests showed that downward displacements were significantly larger than upward ($p = .006$), and rightward were significantly larger than leftward displacements ($p_{\text{right}} = .003$). We ran a repeated measures ANOVA to examine the post-blink gaze position between blink types across experiment phase in each participant. The main effect between voluntary and reflexive blinks was not significant, $F(1, 36) = 1.02, p = .32, \eta_p^2 = .03$. The interaction between blink types and phase was not significant.

Figure 2.2.3. Time-course of gaze positions for voluntary blinks in Experiment 2.3. Baseline – blinks #1–20. Black arrows depict the direction of the dot displacement: a) Upward, b) Downward, c) Leftward, & d) Rightward. Dot was displaced by 0.7° . Error bars represent SEM. Positive values in the figure reflect gaze position in the same direction as the displaced dot. Gaze position after a blink gradually shifted towards the dot position, showing adaptation. This effect was evident in most displacement directions.

Figure 2.2.4. Time-course positions for reflexive blinks in Experiment 2.3. Blink adaptation in the reflexive blinks follows the same trend as in voluntary blinks (Figure 2.2.3) but is less pronounced.

Figure 2.2.5. Average post-blink gaze positions for each phase of Experiment 2.3 for a) voluntary/spontaneous blinks, and b) reflexive blinks. Symbols indicate individual participants. The colors of the bars represent the different displacement directions of the fixation dot during each blink in the adaptation phase (e.g. red = upward displacement). The gray dotted line shows the actual displacement of the target dot (0.7°). Error bars are standard errors of the mean. *** $p < .001$, ** $p < .01$, * $p < .05$. Blink adaptation occurs for all four directions in voluntary/spontaneous blinks, however with widely differing adaptation magnitudes across different displacement directions. In reflexive blinks, adaptation was only significant for rightward displacements.

2.2.5.2: Experiment 2.4

For Experiment 2.4, the baseline again showed no change of post-blink gaze from the pre-blink gaze for both eyes. One-way ANOVAs did not indicate differences

in the baseline across directions for the left eye, $F(3, 47) = .97$, $p = .42$, and the right eye, $F(3, 47) = .77$, $p = .52$. When the fixation stepped during a blink, there were positive biases in the post-blink gaze position towards the new fixation position (Figure 2.2.6). This bias persisted after the adaptation phase in each eye. For the left eye, there were significant differences for the phases of each run, $F(3, 176) = 11.07$, $p = 1.07 \times 10^{-6}$, $\eta_p^2 = .19$ (Figure 2.2.6a).

The planned comparisons t -tests showed blink adaptation for all directions; Upward: $t(11) = -2.57$, $SD = .39$, $p = .03$, gain = 59.59%; Downward: $t(11) = -6.07$, $SD = .54$, $p = 8.04 \times 10^{-5}$, gain = 106.29%; Leftward: $t(11) = -5.23$, $SD = .16$, $p = .2.83 \times 10^{-4}$, gain = 48.76%; and Rightward: $t(11) = -11.03$, $SD = .11$, $p = 2.77 \times 10^{-7}$, gain = 54.55%; however, the upward displacement direction did not survive Bonferroni-corrected $\alpha = .017$. There were no significant differences for the direction of the dot displacement, $F(3, 176) = .26$, $p = .86$, $\eta_p^2 = .004$. The interaction between direction and the phase of each run was not significant.

In the right eye (Figure 2.2.6b), the 4x4 ANOVA illustrated significant differences for the phase of each run, $F(3, 176) = 9.61$, $p = 6.53 \times 10^{-6}$, $\eta_p^2 = .16$. Planned comparisons t -tests on the right eye data showed significant blink adaptation for all directions: Upward: $t(11) = -4.18$, $SD = .40$, $p = .002$, gain = 66.79%, Downward: $t(11) = -3.53$, $SD = .50$, $p = .005$, gain = 80.47%, Leftward: $t(11) = -9.37$, $SD = .12$, $p = 1.42 \times 10^{-6}$, gain = 34.51%, and Rightward: $t(11) = -3.85$, $SD = .31$, $p = .003$, gain = 76.62%. The post-blink gaze position was also significantly different for displacement directions, $F(3, 176) = 3.36$, $p = .02$, $\eta_p^2 = .06$. Post-hoc tests with Bonferroni-corrected α illustrated that the leftward displacement direction was significantly different than the rightward displacement direction ($p = .02$). There was

no difference between the upward and downward displacements. There was no significant interaction effect between the direction and the phase of each run.

Figure 2.2.6. Mean gaze positions after a blink in Experiment 2.4 for a) Left eye, and b) Right eye. Both eyes show blink adaptation in all directions (Late vs. Base). . *** $p < .001$, ** $p < .01$, * $p < .05$.

We then conducted a repeated-measures ANOVA to examine whether the adaptation magnitude differed across each eye. Mauchly's test of sphericity was

violated; $\chi^2(5) = 19.87, p = .001$. Thus, the following analysis utilized Greenhouse-Geisser corrections. The ANOVA showed significant differences for the phase of the run across both eyes $F(2.59, 227.57) = 71.58, p < .001, \eta^2 = .45$. The interaction between eye and direction was not significant. Post-hoc analyses with Bonferroni-corrected α indicated that the early ($p < .0001$), late ($p < .0001$), and post ($p < .0001$) blinks were significantly different from the baseline blinks in each eye. The post-blink gaze positions of the left eye did not differ significantly from the post-blink gaze positions of the right eye ($p = .89$).

Discussion

2.2.6: Blink adaptation occurs in all directions and in both eyes

When a dot steps repeatedly and consistently from its original position during a blink, the oculomotor system learns about this change. The gaze position after the end of each blink gradually adapts over repeated blinks and is shifted towards the displaced position of the dot, even when we cannot see the displacement. We found evidence of this blink adaptation for all displacement directions tested. We tested whether blink adaptation was elicited by reflexive as well as voluntary/spontaneous blinks in Experiment 2.3. While our data showed significant adaptation in reflexive blinks only when the dot stepped towards the right, the repeated-measures ANOVA did not show significant differences between voluntary and reflexive blinks. Finally, we measured blink adaptation in both eyes for four displacement directions in Experiment 2.4. We found that adaptation occurred in both eyes, with some interesting anisotropies for temporal and nasal directions of adaptation.

2.2.6.1: Adaptation magnitude is unequal across directions

Our findings add to the initial report on blink adaptation by Maus et al. (2017). We show here that blink adaptation occurs for dot displacements in any of the

directions tested. However, adaptation magnitude is not isotropic; we found larger adaptation for rightward and downward displacements.

The larger adaptation for downward directions may be explained by the nature of blink-related eye movements. During a blink while the eyelids are closing, the eyes move inward nasally and downward concurrently (Bour, Aramideh, & De Visser, 2000; Collewyn et al., 1985). This motion is universal regardless of the kind of blinks (i.e., spontaneous, voluntary, or reflexive blinks). Before the eyelids cover the eyes, the eyes return from the downward position to their previous position (Riggs et al., 1987). Based on this blink-related eye movement, it is possible that the eyes do not fully return to the previous position for a downward displaced dot. Instead, the eyes are more likely to stop at the predicted dot position resulting in a larger adaptation gain observed.

To measure reliable blink adaptation for upward displacements, more adaptation trials might be required. Maus et al. (2017) reported that adaptation for rightward displacements began to plateau after ~35 blinks. We replicated a similar pattern in our rightward adaptation. However, the blink quantity required for adaptation to plateau was different across the four directions. In the time-course plots for upward displacements in voluntary blinks (Figure 2.2.3), the gaze position after a blink never truly plateaued. This meant that the small adaptation magnitude for the upward displacement might be attribute to two factors, namely, (i) adaptation in the upward direction appears slower, i.e., it requires more adapting blinks to reach a plateau, or (ii) the vertical component of blink-related eye movements reduces the effects of adaptation. In Experiment 2.4, where participants spent 60 blinks to induce adaptation compared to only 40 blinks in Experiment 2.3, we already see somewhat more robust blink adaptation in the upward direction.

Our present eye gaze recording method relies on video-based eye trackers. Therefore, we cannot ascertain which phase of blink-related eye movements is altered by adaptation, since the tracker does not provide information about the orbit's rotation while the lid is closed. Further research using search coils (as e.g. by Khazali et al., 2016; Khazali et al., 2017) might better elucidate what the eye is doing during an on-going blink.

Regardless of the differences in upward and downward adaptation magnitude, it is essential to point out that similar differences are also observed for vertical saccades. Collewyn et al. (1988b) showed that when participants made 10° – 70° vertical saccades, upward saccades tended to undershoot the target, whereas downward saccades tended to overshoot the target. We observed similar anisotropies for blink adaptation in the absence of saccades. These anisotropies seem to be general for many different cases of eye movements, hinting at general anatomical behaviors for eye movements in different directions.

2.2.6.2: Possible adaptation in reflexive blinks

The lack of significant blink adaptation for reflexive blinks does not suggest that blink adaptation is unique for voluntary/spontaneous blinks. The adaptation magnitude for both the voluntary and reflexive blinks in Experiment 2.3 showed a similar pattern throughout the phases of the experiment (Figure 2.2.5b). Furthermore, the repeated-measures ANOVA showed no significant differences between the two blink types, although adaptation in the reflexive blink condition was weaker.

Weaker adaptation in the reflexive blink condition might be due to contamination by spontaneous blinks during the adaptation phase. Participants might have blinked spontaneously, not only when an air-puff was delivered. Thus, reflexive blinks were interspersed with spontaneous blinks. Furthermore, participants may have

blinked several times following a puff. Since these additional blinks were not paired with a target step in the same way as the reflexive blinks triggered by an air puff, adaptation may have been diluted by these additional blinks. Blink adaptation in Maus et al. (2017) was rather short-lived; the effect was extinguished after just 4-5 blinks without a target step. These factors help explain the lack of significant findings in the reflexive blink condition.

Since adaptation in reflexive and spontaneous/voluntary blinks overall followed a similar pattern, it is likely that the adaptation occurs in general blink circuitry, and not in mechanisms exclusive to either blink type. To better examine how blink adaptation differs between the types of eye blinks, a different method for eliciting reflexive blinks could be used. For instance, the orbicularis oculi (OO) nerve located above the eye brows could be stimulated electrically to induce reflexive blinks (Kimura, Powers, & Van Allen, 1969; Shahani, 1970).

2.2.6.3: Binocular differences in blink adaptation

The stark contrast between adaptation magnitudes in the horizontal direction in Experiment 2.3 suggests that blink adaptation favors changes of eye gaze in the temporal and not nasal direction. In Experiment 2.3 we recorded only the right eye and found a strong bias for rightward adaptation to reach larger magnitude than leftward adaptation. These results are consistent with past findings in which eye movements towards the temporal direction tend to be greater than movements in the nasal direction (Collewyn et al., 1988a). To further investigate this, we recorded binocular eye movements in Experiment 2.4. If blink adaptation were stronger for temporal directions, we would expect to find the opposite pattern in the left eye. This was, however, only partially supported. We found that the adaptation magnitude for both leftward and rightward displacements in the left eye were equivalent, whereas we

replicated the anisotropy for the right eye. Nonetheless, left displacements led to larger adaptation magnitude in the left eye than in the right eye, and conversely right displacements led to larger adaptation magnitude in the right eye than in the left eye.

2.2.6.4: Saccadic and blink adaptation

Our results shed light on possible parallels between blink adaptation and saccadic adaptation. Despite the lack of fast ballistic movements, the oculomotor system can adapt to position changes during a blink. This adaptation seems to be indifferent for spontaneous, voluntary, or reflexive blinks. However, some questions remain unanswered. For instance, saccadic adaptation occurs under “random-walk” sequences of saccades with different directions, as long as the target is displaced in the direction of the saccade (Rolfs, Knapen, & Cavanagh, 2010). One could test whether random-walk positional changes during blinks would also elicit blink adaptation. Since adaptation can be transferred to other saccades within a certain spatial field (Collins, Doré-Mazars, & Lappe, 2007), another potential experiment would be to investigate whether such an adaptation field is also present for positional changes across eye blinks.

2.2.6.5: Does blink adaptation maintain perceptual continuity?

Blink adaptation may be an oculomotor behavior that maintains perceptual continuity. Awareness reduces the effects of adaptation (Blake, Tadin, Sobel, Raissian, & Chong, 2006; Stein & Sterzer, 2011) but does not fully eliminate adaptation (Adams, Gray, Garner, & Graf, 2010). Participants who were aware of the displacements also showed adaptation. If blink adaptation was not a behavior that maintains perceptual continuity, it should be absent when participants realized the displacements. Regardless, the role of blink adaptation on perceptual continuity warrants further tests. For instance, blink adaptation may be driven by visual errors. In

saccade literature, visual errors elicit saccadic adaptation (Noto & Robinson, 2001; Wallman & Fuchs, 1998). Saccadic adaptation decreases for inconsistent visual errors (Havermann & Lappe, 2010). Adaptation occurs even if visual errors are presented 1–2 s after a primary saccade (Srima & Curtis, 2010). If blink adaptation parallels saccadic adaptation, future studies can investigate blink adaptation in the absence of visual errors.

It is uncommon for objects to move only during a blink in the natural environment. The fact that most participants ($N = 17$, 85%, Experiment 3, and $N = 6$, 50%, Experiment 2.4) were unaware of the displacements suggests that we do not expect objects to move only during the blink. It would be detrimental to perception if small positional changes during the blink were perceived as novel. Our perception of the object's position after the blink is likely a continuation from the information before the blink due to our expectation. We may be unaware if the object indeed moved during the blink because the oculomotor system is maintaining perceptual continuity through blink adaptation. Small position changes are reduced, and we may not detect them because the object's position before and after the blink appears alike. Hence, this oculomotor behavior can help to ensure the object's position information is continued across the blink.

2.2.6.6: Interim summary

Regardless of whether blinks were spontaneous, voluntary, or reflexive, we found evidence of anticipatory corrective eye movements during blinks when a dot was displaced in the cardinal directions. This suggested that the type of blink is irrelevant if an eye blink is made. Anisotropies in blink adaptation are consistent with well-known directional biases in saccades, suggesting that anatomical oculomotor constraints also apply to adapted blink-related eye movements. Continuity of a target's

position is preserved across the blink because the oculomotor system corrects for positional changes when blinking.

General discussion for part 2

2.3.0: Expected effect sizes and confidence intervals between our study and existing studies

We did not recruit the same number of participants as the original study (Maus et al., 2017). In this section, we calculated the expected effect sizes and confidence intervals between our experiment and the original study. We limited our calculations to rightward displacements at the late adaptation phases based on the original study. We computed a non-directional two-tailed Cohen's d (J. Cohen, 1988). The formula was $d = |M_1 - M_2| \div s$, where $M_1 = 0$ (Experiments 2.1–2.2) or baseline (Experiments 2.3–2.4), M_2 = means from late phase, and s = pooled standard deviation. The formula for pooled standard deviation was $s = \sqrt{\frac{SD_1^2 + SD_2^2}{2}}$, where SD_1 indicates $SD = 1$ (Experiments 2.1–2.2) or baseline (Experiments 2.3–2.4), and SD_2 indicates SD from late phase. We reasoned that if there was no adaptation in Experiments 2.1–2.2, then $M_1 = 0$ and $SD_1 = 1$. Thus, d indicated the effect of our study as compared to 0 (no adaptation, Experiments 2.1–2.2) or the baseline (Experiments 2.3–2.4).

Like in 1.5.0, we did not conduct power analysis because post-hoc power analysis is inappropriate and not good practice. Instead, we computed the 95% confidence intervals, $\bar{x} \pm t \times \frac{s}{\sqrt{n}}$, where $\bar{x}$ = sample mean, $s = SD$ and n = sample size. t values were taken from a t -distribution table for two-tailed distributions at $\alpha = .05$. This alpha level indicated a 95% chance to correctly reject a true null hypothesis. The 95% confidence intervals illustrated the range of values that would also be observed in the population with 95% certainty.

2.3.1: Results for expected effect sizes and confidence intervals

Table 2.1 shows the expected effect sizes and 95% confidence intervals between our studies and existing studies. There were medium to large effect sizes across the different experiments. However, large effect sizes did not mean there was blink adaptation in the population. The confidence intervals for Experiment 2.1 and 2.2 included null (i.e. 0). When this happens, we are unable to reject the null hypothesis. This signified that there were no observed effects in the population, even though the effect sizes for the two experiments were large.

Table 2.1. Effect size and confidence intervals between current experiments and Maus et al. 2017 for rightward displacements

Experiment 2.1 – Voluntary blinks			Maus et al. (2017), 0.5° displacement		
<i>d</i>	N	Means (C.I.)	<i>d</i>	N	Means (C.I.)
.49	4	.36° (-.04 – .76)	.49	5	.35° (.29 – .41)
Experiment 2.2 – Reflexive blinks					
.32	4	.23° (-.14 – .60)			
Experiment 2.3 – Voluntary blinks					
.78	10	.57° (.38 – .76)			
Experiment 2.3 – Reflexive blinks					
.47	10	.34° (.17 – .51)			
Experiment 2.4 – Left eye					
.48	12	.35° (.22 – .48)			
Experiment 2.4 – Right eye					
.63	12	.46° (.30 – .62)			

d = non-directional effect size using Cohen's *d*, N = number of participants, C.I. = 95% confidence intervals.

2.3.2: Revisiting whether modality-specific temporal stability is a failure of change detection

In part 1, we showed that temporal stability could be expressed in serial dependence. The nature of the information that was compared appear to be embedded

in perception. This was because we observed visual serial dependence even when participants reported auditory vowels on the previous trial. Visual perception was kept continuous and stable across two perceptual sampling (i.e. stimulus presentation). Therefore, this indicated that temporal stability could be modality-specific.

In part 2, we limited our investigations to the visual domain since temporal stability could be modality-specific. We then asked why we do not perceive instability after each blink, since we blink very often. One possibility for the lack of instability was that temporal stability simply ignores endogenous disruptions (i.e. the blink). While one may argue that temporal stability across blinking is achieved because the blackouts are visually suppressed, it is unlikely so, because we can perceive the act of blinking, but we do not perceive the instability of the visual world. Therefore, visual suppression from the blink cannot explain why perception is continuous over time.

Temporal stability may be a failure of change detection. This makes sense because undetected changes often appear continuous. In change blindness experiments, scene perception appears stable even if physical changes occur. This is because observers do not immediately detect the change when searching for the change. While searching for the change, hysteresis could cause the scene percept to be sluggish and object updating could be constantly updating object representations in the scene. These could then make change detection difficult. Hence, temporal stability is achieved, and perception becomes continuous over time because changes are undetected.

The problem with arguing that temporal stability is a failure of change detection arises when we return to blinking. Perception is continuous and stable over time, even after blinking. Blinking also causes gross disruptions to the visual world. Although blackouts from blinking are visually suppressed, the eyes do not return to the

same identical position after each blink (Collewyn et al., 1985; Riggs et al., 1987).

This translates into different retina images before and after blinking. One may assume that changes before and after blinking are not detected and be contented that temporal stability is the result of undetected changes. However, if this were true, we would not observe blink adaptation and our gaze would not adapt to object displacements during the blink. Therefore, this suggests that temporal stability requires something else besides change detection.

2.3.3: Temporal stability is reached by recruiting systems to ensure stability

Temporal stability is reached by recruiting systems to ensure stability. This rationale stemmed from the findings in part 2, where we showed blink adaptation across all four directions. Importantly, both eyes displayed adaptation, and there were noticeable anisotropies. Although there was no significant adaptation for reflexive blinks, the data trended in a similar fashion as voluntary/spontaneous blinks.

Temporal stability is achieved in vision by recruiting the oculomotor system to minimize discrepancies of an object's position before and after blinking. This oculomotor system's behavior cannot be explained by object updating or hysteresis. We perceive objects by looking at them. According to object updating, object representations are updated from constant sampling (Enns et al., 2010). When the object changes positions, the object representation is updated. However, object updating does not explain why the oculomotor system corrected gaze positions toward the object's new position. Hysteresis would unlikely explain the oculomotor system's behavior, since a persistent perceptual state would likely cause the gaze to be uncorrected and fixated on the old object's position. Therefore, by recruiting the oculomotor system, our gaze is repositioned onto positional changes of the object, sustaining temporal stability.

We speculate that the oculomotor system's behavior could be explained a signal which anticipates the eye positions after blinking. Before the blink, the perceptual system receives the current percept of the dot. During the blink, the perceptual system ignores the endogenous disruption from blinking. Since the blink is now in motion, a signal is then generated in the oculomotor system to predict where the eyes would be after the blink ends. After blinking, the dot was displaced, and there is now a disparity between the two percepts. The perceptual system activates the oculomotor system to remedy the disparity by adjusting the gaze toward the displaced dot position. The oculomotor system uses a signal that anticipated eye positions after blinking to re-orient the gaze. Therefore, temporal stability is ensured because the discrepancy between an object's position before and after the blink is minimized.

Part 2 conclusion

Part 2 raised the question whether temporal stability was a failure of change detection. This was motivated by observations where frequent blinking does not cause the visual world to appear unstable. If temporal stability were a result of undetected changes, we would experience instability after each blink. According to the literature, humans blink frequently, and vision is suppressed during the blink. However, visual suppression could not explain temporal stability. This suggested that temporal stability may ignore endogenous disruptions from the blink.

There are many reasons why we experience change blindness, and why we are bad at detecting changes. For instance, we are bad at change detection because we are unaware of changes. If temporal stability could be explained by the shortcomings of change detection, there would be no blink adaptation because there is no need for the oculomotor system to correct for gaze when an object changes positions across a blink. However, such corrections exist during blink adaptation, regardless if the observer was

aware of the change. Thus, we concluded from the results that the oculomotor system shifted gaze towards systematic changes during the blink. Since perception is continuous after blinking, it suggests that temporal stability involved more than change detection. Temporal stability in vision is successful because other systems (i.e. the oculomotor system) are involved to ensure that perception remains continuous.

When small systematic positional changes occur during the blink, we are unlikely to notice them because of blink adaptation behaviors. We may become unaware of changes since the gaze is orientated towards the object's new position after blinking. The re-orienting of gaze could be due to a blink-related signal that anticipates the eye positions after blinking. The discrepancies in the object's position before and after the blink become minimized and the object appears to be in the same position. From this, we argued that temporal stability was not only the lack of change detection. Stability in vision was reached by involving the oculomotor system to help maintain stability. This could be because the oculomotor system used a signal created during the blink to shift gaze to positional changes of an object after blinking.

Part 3 – Comparing endogenous disruptions in parts of the oculomotor system**3.0.0: Introduction to part 3**

Part 2 showed that temporal stability in vision was successful because the oculomotor system was involved to maintain stability. Specifically, the oculomotor system had oriented gaze towards new object positions after blinking. Temporal stability was not just a failure of change detection because the oculomotor system was involved to ensure continuity of an object's position following endogenous disruptions to the visual world. We speculated that the oculomotor system could re-orient the gaze due to a signal which anticipated the eye positions after blinking. Thus, temporal stability was maintained by the oculomotor system thanks to this signal. Could our speculation be true?

Besides blinking, the oculomotor system is also involved in moving our eyes. Eye movements, called saccades, are fast, ballistic movements that we make to explore the visual environment (Becker & Fuchs, 1969). The visual system processes snapshots of what we see between each saccade but suppresses information during the saccade. Yet, the world remains continuous (Rolf's, 2015). If our speculation is true, that the oculomotor system re-orient's the gaze due to a signal which anticipated the eye positions after blinking, then this signal may also influence saccades because saccades and blinks belong to different arms of the oculomotor system. To better understand this, we must appreciate the nature of saccades and recognize the intricacies behind the oculomotor system's role in saccades and blinks.

Temporal stability in vision could be reached by the oculomotor system because of the signal which expected the eye positions after blinking. This signal also affected saccades. We showed evidence of this by studying saccades disrupted by blinks. Saccades are planned movements. Saccade start positions are affected when we

blink before launching the saccade. This is because the eyes do not return to the exact same position after blinking (Collewijn et al., 1985; Riggs et al., 1987). If the start position changes and the oculomotor system does not update the plan, then the saccade would never reach the destination. We showed that this was not the case because saccades to visible targets were more accurate after blinking. This suggested that the oculomotor system updated the saccade plan to ensure the saccade remain accurate. Updating could be an oculomotor behavior which maintains perceptual continuity during visual exploration by ensuring that our eyes arrive at where we intend to look regardless of endogenous disruptions from blinking. This was possible due to the signal which anticipated eye positions when blinking.

In the following sections, we presented the literature pertaining to the nature of saccades and compare blinks to saccades. Then, we briefly examined how saccades contributed to perceptual continuity.

3.0.1: The nature of saccades

Saccades are ballistic eye movements that cannot be interrupted voluntarily once launched (Becker & Fuchs, 1969). They tend to undershoot the target (Collewijn et al., 1988a, 1988b). We normally do not make saccades beyond 15° in the natural world (Bahill, Adler, & Stark, 1975). Very large saccades are often accompanied by head movements (Stahl, 1999). Saccades are determined by their *main sequence* (see Figure 3.0.1): the relationship between saccade amplitude and either duration or peak velocity (Bahill, Clark, & Stark, 1975b). Velocities increase linearly with size $< 10^\circ$ (Boghen, Troost, Daroff, Dell'Osso, & Birkett, 1974). The increase becomes nonlinear and plateaus at larger sizes (Baloh, Konrad, Sills, & Honrubia, 1975). Peak velocity and acceleration for horizontal saccades asymptotes from 40° (Collewijn et al., 1988a). Acceleration for vertical saccades plateaus after 40° although velocity continues

increasing with size (Collewyn et al., 1988b). These properties do not apply for unrestrained heads (Freedman & Sparks, 2000). These saccade characteristics do not interfere with how saccades are described or classified.

Figure 3.0.1. Horizontal saccade main sequence using amplitude and velocity. Taken from Baloh et al. (1975), Figure 1. Data of a single observer for binocular and monocular recording. Amplitudes are measured in degrees. The constants K and L are derived from a curve-fitting program. The sum of squares (Sum sq) indicate goodness-of-fit of the exponential curve. The observer was tasked to make leftward or rightward saccades.

3.0.2: Saccade classifications

There are many ways to describe saccades. Saccades can be classified by the order of occurrence: *primary*, *secondary*, etc. Secondary saccades normally move in the same direction as primary saccades (Becker & Fuchs, 1969). Saccades are sometimes described by their role. For example, saccades which correct for under/overshoots are called corrective saccades (Prablanc & Jeannerod, 1975). Larger undershoots are usually corrected quicker than smaller undershoots and the peak latency for correction is ~60 ms (Deubel, Wolf, & Hauske, 1982). Recent evidence

shows that corrective saccades can arise without visual feedback (Bonnetblanc & Baraduc, 2007; Ohl, Brandt, & Kliegl, 2013). Specifically, corrective saccades happen when saccade landing errors (i.e. the distance between saccade landing position and the target position) exceed 10° in the absence of visual feedback (Tian, Ying, & Zee, 2013).

Saccades are also discriminated by what elicits the saccade. Visually guided saccades (VGS) are saccades directed at visible objects. VGS are retinotopic and will always be directed to the stimulated retinal site regardless of the saccade start position (Robinson, 1972). Memory-guided saccades (MGS) are saccades made to remembered target locations. MGS tend to overshoot the target (Ohtsuka, Sawa, & Takeda, 1989) and could be encoded in the memory from information surrounding the target (Becker & Jürgens, 1979; E. Zimmermann, Burr, & Morrone, 2011).

Reflexive or express saccades are saccades to attention-grabbing stimuli (B. Fischer, 1986). These saccades have very short latencies, between 85–140 ms when the stimulus appears (B. Fischer & Ramsperger, 1984). Anticipatory saccades are saccades which begin 100–120 ms before an event (Kalesnykas & Hallett, 1987) because of predictable targets or long latencies before the cue to saccade (Findlay, 1981). Micro-saccades are very small but high velocity gaze shifts as small as $7'$ (Winterson & Collewyn, 1976), although modern definition using video-based trackers have reached a consensus of $\sim 1^\circ$ to capture over 90% of micro-saccades (Martinez-Conde, Otero-Millan, & Macknik, 2013). We make 1–2 micro-saccades each second (Martinez-Conde et al., 2013; Rolf, 2009) and micro-saccades help protect visual signals from degradation during fixation (Martinez-Conde, Macknik, Troncoso, & Dyar, 2006).

In summary, saccades are fast ballistic movements with a distinct main sequence. Saccade velocity/duration is dependent on saccade size. There are many ways to describe saccades based on the kinematical, purpose, or behavior of the saccade. In the next section, we examine what is involved behind moving our eyes.

3.0.3: Saccades: from intention to movement

The oculomotor system begins planning a saccade the moment we decide to make one. The frontal eye field directs the intention to make a saccade (Fuchs, Kaneko, & Scudder, 1985; Lu, Matsuzawa, & Hikosaka, 2002; Robinson, 1981). Saccade commands which initiate saccades (Sparks & Mays, 1990) originate from burst-like activity in the superior colliculus ~20 ms before the saccade (Sparks, 1978; Wurtz & Goldberg, 1971). Distinct burst neurons fabricate a combination of burst activities (Scudder, Kaneko, & Fuchs, 2002) and produce different saccades types (Goossens & Van Opstal, 2006; Lee, Rohrer, & Sparks, 1988).

From the superior colliculus, the saccade command travels to the premotor neurons in the brainstem (e.g. reticular formation). Excitatory premotor neurons in the ipsilateral paramedian pontine reticular formation and the rostral interstitial medial longitudinal fasciculus controls horizontal (Hepp & Henn, 1983; Zhou & King, 1998) and vertical (Vilis, Hepp, Schwarz, & Henn, 1989) saccades respectively. Saccade trajectory is determined by short-, medium-, or long-led burst activity from these premotor neurons (Horn, Büttner-Ennever, & Büttner, 1996; Missal, De Brouwer, Lefèvre, & Olivier, 2000; Scudder, Fuchs, & Langer, 1988). Burst activity also travels to the omnipause neurons in the brainstem (Büttner-Ennever, Horn, Henn, & Cohen, 1999; N. J. Gandhi & Keller, 1997). Omnipause neurons discharge during fixation and ceases activity during saccades (Everling, Paré, Dorris, & Munoz, 1998; Evinger, Kaneko, & Fuchs, 1982).

Extraocular motoneurons receive burst and sustained activities from premotor neurons in the brainstem and executes the saccade. Motoneurons innervate the extraocular muscles in the eye and orbit (Goldberg & Shall, 1999). Motoneurons demonstrate *pulse-slide-step* activities (Scudder et al., 2002), mimicking discharge patterns from premotor neurons in the brainstem (Fuchs et al., 1985). Extraocular muscles move the eye once they received the *pulse* activity (Munoz, 2002). The higher the number of pulses, the larger the saccade amplitude (McFarland & Fuchs, 1992).

Saccades must overcome mechanical forces such as torque and inertia (Haslwanter, 2002; Westheimer, 1954). The exchange between mechanical forces, muscle movements, and viscous elements during the saccade is hypothesized to be equilibrated by the *slide* activity (Miller & Robins, 1992). The exact nature of the *slide* activity is still unknown as it is observed in many types of burst neurons (Scudder et al., 2002). The *step* activity is likely derived from omnipause neurons and relayed through inhibitory neurons (Strassman, Highstein, & McCrea, 1986) to hold the eye in its current position. The cerebellum modulates the pulse and step activity to coordinate the eyes during saccades (Fuchs et al., 1985; Optican & Robinson, 1980).

In short, we plan saccades the moment we intend to make one. The intention, originating from the frontal eye field, projects to the superior colliculus. Burst neurons in the superior colliculus generate activity which travels down to premotor neurons in the brainstem, before arriving at motoneurons that innervates extraocular muscles. These neurons show pulse-slide-step activities which tell extraocular muscles to move our eyes or to hold them in position.

3.0.4: Saccades and perceptual continuity

Visual information is suppressed during saccades (Burr et al., 1994; Richards, 1969). However, we do not perceive the visual world as a series of fixations. Two

theories are selected to explain how perceptual continuity is maintained across saccades. They are trans-saccadic memory and remapping attention.

Trans-saccadic memory refers to the visual memory across a saccade. It has a limited capacity (Prime, Tsotsos, Keith, & Crawford, 2007) and decays (Irwin, 1992). Trans-saccadic memory is integrated across saccades to create a continuous experience of the visual world (Prime, Niemeier, & Crawford, 2006). The stimulus at the end of a saccade appears fused if the features at saccade start and end differ (Paeye, Collins, & Cavanagh, 2017). We tend to perceive what we see at the end of a saccade as continuous even if the information is different before the saccade started (Deubel, Schneider, & Bridgeman, 2002). This is because information across saccades accumulates to form a stable representation of the visual environment (Melcher & Morrone, 2007).

Perceptual continuity across saccades is maintained when attention is remapped (Cavanagh, Hunt, Afraz, & Rolfs, 2010). Features such as orientations or colors which are presented at the remapped location are reported accurately before the saccade begins (Jonikaitis, Szinte, Rolfs, & Cavanagh, 2012; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011). This is because attention is shared between the start and end location of a saccade. Mirpour and Bisley (2015) presented this evidence in macaque lateral intraparietal cortex during a foraging task. The researchers showed that neurons involved with attention switched seamlessly between the pre- and post-saccadic locations to allocate attention. The researchers concluded that attention was allocated between the two saccade locations to maintain equal distribution of attention.

The literature described here is not exhaustive at explaining perceptual continuity across saccades. Although visual information is suppressed during

saccades, the visual world is not a series of fixations. Perception remains continuous across saccades because of trans-saccadic memory and remapping attention.

3.0.5: How saccades relate to blinks

We explore the natural environment by making saccades and blinks. Saccades may relate to blinks because the regions in which they are processed overlap. The intention to move our bodies is thought to originate in the medial frontal cortex (Rushworth, 2008). This area is also activated during voluntary saccades and voluntary blinks (Bodis–Wollner, Bucher, & Seelos, 1999).

Regions involved in producing saccades also moderate blinks. Superior colliculus burst neurons discharge before saccades (Fuchs et al., 1985; Munoz & Wurtz, 1995) but are suppressed by reflexive blinks (Goossens & Van Opstal, 2000b). Inhibiting the superior colliculus during reflexive blinks may prevent the superior colliculus from generating another saccade command. A reflexive blink can occur during a saccade, but not vice versa (Goossens & Van Opstal, 2000a). Superior colliculus burst neurons regulate saccade velocity/duration (Goossens & Van Opstal, 2006; Munoz, Waitzman, & Wurtz, 1996). Saccade velocity/duration are also modified by blinks because blinks inhibit superior colliculus burst neurons (Goossens & Van Opstal, 2000b). For example, saccade velocity and acceleration decreases when blinks occur during saccades (Rambold, Sprenger, & Helmchen, 2002; Rottach et al., 1998).

Saccades and blinks recruit premotor neurons in the brainstem. The lateral geniculate body and ipsilateral paramedian pontine reticular formation elicits saccades and blinks (B. Cohen & Feldman, 1968). The rostral interstitial medial longitudinal fasciculus controlling vertical saccades also activates vertical eyelid movements (Chen & May, 2002). The interstitial nucleus of Cajal carries vertical eye position and

torsional information (Crawford, Cadera, & Vilis, 1991). It also modulates vertical lid positions (Chen & May, 2007). The omnipause neurons cease firing during saccades (Everling et al., 1998) and blinks (Mays & Morriss, 1995). However, omnipause neuron activity predicts the beginning of reflexive but not spontaneous blinks (Schultz, Williams, & Busettini, 2010). Prolonged eye closure which inhibits omnipause neurons decreases saccade velocity (Shaikh et al., 2010).

Motoneurons which control vertical saccades and lid movements share the same discharge characteristics: burst activity initiates saccade/lid movements and tonic activity holds the eye/lid in place (Fuchs, Becker, Ling, Langer, & Kaneko, 1992). Large saccades activate the orbicularis oculi muscles which lowers the eyelid (Evinger et al., 1994). The inferior rectus muscles affect vertical lid movements and vertical saccades (Metz, 1980; von Noorden, 1970).

Blinks and saccades are also processed in higher-order brain regions such as the posterior parietal cortex (Shibutani, Sakata, & Hyvärinen, 1984), brainstem, and cerebellum (Zee et al., 1983). In summary, saccades and blinks are processed by overlapping regions.

3.0.6: The corollary discharge, motor plans, and updating

Saccade planning involves the stimulus identity (Shen & Paré, 2007), eye proprioception (Bridgeman & Stark, 1991), and the saccade destination (Dassonville, Schlag, & Schlag-Rey, 1992). The *Corollary Discharge* is a saccade plan signal which is sent to other brain regions to signal an impending eye movement (Sperry, 1950; Wurtz, 2008). Corollary discharge is an important signal which contributes to perceptual continuity. The oculomotor system compares the eye position after the saccade and the corollary discharge to determine if the eyes landed onto the target (Wurtz, 2018). Corollary discharge enables us to distinguish whether targets have

changed positions after the saccade (Deubel, Schneider, & Bridgeman, 1996). Without the corollary discharge, target locations are misreported (Cavanaugh, Berman, Joiner, & Wurtz, 2016). Thus, the corollary discharge helps us evaluate if our eyes are on the target or if the target has shifted after the saccade.

A motor plan is derived from the corollary discharge signal in the saccade plan (Wurtz, 2018). Motor plans direct muscles to specific locations at a certain strength (R. G. Cohen & Rosenbaum, 2004; M. Zimmermann, Meulenbroek, & de Lange, 2011). Motor plans are also updated when movements change before reaching the goal (Seidler, Bo, & Anguera, 2012; Shima, Mushiake, Saito, & Tanji, 1996). This ensures that the muscles reach the goal despite additional movements or alterations.

Saccade plans are updated. This is often illustrated using a double-step paradigm, in which observers make two sequential saccades (Becker & Jürgens, 1979). Double-step paradigms show that multiple saccades are planned in parallel because saccades cannot be stopped once it takes flight (Becker & Fuchs, 1969). However, the saccade can be redirected if the target changes location after the saccade started (Ray, Schall, & Murthy, 2004). Saccade plans are updated and redirected with the help of the posterior parietal cortex (Medendorp, Goltz, Vilis, & Crawford, 2003). Updating occurs no earlier than 150 ms before the saccade begins (Bellebaum, Hoffmann, & Daum, 2005). The oculomotor system updates target positions as quickly as 40 ms when the target appears (Kosovicheva, Wolfe, & Whitney, 2014). Remembered positions are also updated in anti-saccades (Medendorp, Goltz, & Vilis, 2005).

In short, the corollary discharge is a saccade planning signal which tells other brain regions of an upcoming movement. Motor plans are then derived from the

corollary discharge signal. Motor plans are updated whenever there are unexpected changes/movements to ensure that the muscles will arrive at the correct destination.

3.1.0: Saccade planning and blinks

So far, our review of the literature suggested that blinks and saccades could be interlinked within the oculomotor system. We speculated, in part 2, that a signal which anticipates the eye position when blinking exists within the oculomotor system. Is our speculation true? We can examine this by comparing whether saccade plans are updated whenever there is a blink. The goal of the oculomotor system is to guide the saccade towards the target. Perception is continuous if we look at what we want. The oculomotor system creates a saccade plan to direct our eyes. If our speculation is true, then blinking before the saccade would cause the saccade plan to be updated/recomputed. This is because our eyes also move during a blink. When fixated straight-ahead, both eyes rotate nasally inward and downward simultaneously as the blink begins. The eyes return to its approximate position before the lid covers the eye (Collewyn et al., 1985; Riggs et al., 1987). Blinks also sometimes occur in conjunction with saccades because large saccades activate muscles which lower the eyelids (Evinger et al., 1994). Thus, we can ask the following: are saccade plans updated if the observer blinks before making the saccade? Updating would provide evidence that there is a signal which anticipates eye positions after blinking, and that this signal also affect subsequent saccades. This is because the blink-related arm of the oculomotor system is signaling the saccade-related arm of the oculomotor system that an endogenous change has occurred. Hence, the saccade plan is updated to ensure that saccades always land on the target.

We cannot keep our eyes completely stable. We make involuntary eye movements such as tremors, drifts, and other fixational movements (Hess, Reisine, &

Dürsteler, 1985; Martinez-Conde et al., 2006; Poletti & Rucci, 2016; Rolfs, 2009).

These movements create fixational errors if our eyes move off the fixation. Fixation errors are corrected by drifts (Cyr & Fender, 1969), micro-saccades (Engbert & Kliegl, 2004), and blinks (Khazali et al., 2017) when the fixation is visible. When the fixation point is absent, fixation errors increase rapidly and plateau after 2° , but is never corrected (Skavenski & Steinman, 1970). Saccade plans are updated in relation to the goal position. Thus, fixation errors do not determine saccade accuracy to visible targets because the target, rather than the start position, guides the saccade landing position (Robinson, 1972). This suggests that the initial eye position is unimportant as compared to the goal during saccade planning (Vergilino & Beauvillain, 2000). However, we cannot measure saccade planning or updating by looking only at saccade accuracy to visible targets. We can better infer saccade planning or updating by contrasting saccade accuracy between remembered and visible targets.

When both the fixation and target are absent, fixational errors to a remembered fixation position could influence saccades to a remembered target. Hence, it is possible that the starting position of the saccade is equally as important for invisible targets. Are saccade plans updated if both the fixation and target are absent after the plan was created? In other words, after planning the saccade plan, do fixational errors over time predict saccade accuracy when both fixation and target are invisible?

3.1.0.1: Experiment 3.1 tests saccade planning when blinks occur, and if fixational errors predict saccade accuracy

The purpose of the experiment was to investigate if blinks update saccade planning, and whether fixational errors predict saccade accuracy after saccade planning. We asked if the planned saccade was updated after the blink due to

movements introduced by the blink. Observers planned a saccade once the target position was available. They then blink before making a saccade to the target.

We hypothesized that blinks update the saccade plan. If blinks update the saccade plan, then the saccade would be accurate despite blinking. However, if the saccade was less accurate after the blink, then the saccade plan was not updated. This was because the eyes do not return to the same position after the blink. As such, the saccade after the blink started at a new position which did not correspond to the position in the saccade plan. Since the plan was not updated, the saccade did not land accurately on the target. We also assessed whether fixation errors could predict the saccade after planning. If fixational errors over time predicted saccades, then this would suggest that the eye position information was involved in updating the saccade plan.

In the following experiment, we recruited participants to make VGS or MGS in blink and no-blink conditions. Saccade direction was randomized throughout the experiment. Fixation and targets were always 10° apart and presented in a random-walk fashion. The first hypothesis was evaluated by comparing saccade accuracy across conditions (blink/no-blink) and saccade types (VGS/MGS). If blinks influenced saccade planning, then saccades should be more accurate in blink than no-blink conditions. The second hypothesis was tested by evaluating if fixation errors predicted the saccade after saccade planning. If fixation errors over time predicted saccades, then fixation errors influenced saccade plans. Alternatively, if fixation errors did not predict saccades, then they did not affect saccade plans.

Methods

3.1.1 Participants

The number of participants for this study was based on those in Experiment 2.3 and Experiment 2.4. Participants ($N = 13$, $M = 25.92$ years old, $SD = 3.43$, 3 females)

were recruited from Nanyang Technological University. They were naïve to the purpose of the experiment and had no experience with eye tracking experiments, except for one. Participants had normal or corrected-to-normal visual acuity and no hearing problems. Consent was given before the experiment. Upon completion, participants were rewarded S\$10/hr. The experiment was approved by Nanyang Technological University's Institutional Review Board.

3.1.2: Apparatus

The experiment was programmed in MATLAB (Mathworks Inc., Natick, MA, USA), with Psychtoolbox 3 (Brainard, 1997; Kleiner et al., 2007). The display was a 20" Sun Microsystems CRT monitor, resolution 1152 x 864, and 100 Hz refresh rate (black = 0.75 cd/m², white = 132 cd/m²). The chin rest was ~65 cm from the monitor and the eye tracker was Eyelink 1000+ (SR Research, Ottawa, Ontario, Canada). We tracked the right eye at a sample rate of 1000 Hz and the tracker was calibrated using a 5-point procedure. Viewing remained binocular. A command was sent to the tracker to perform drift correction on every trial automatically. We compared the gaze position to the fixation stimulus position. The tracker was re-calibrated with the full 5-point procedure if the online gaze data exceeded 3° from fixation.

3.1.2.1: Stimulus and trial sequence

The stimulus was a white dot (diameter = 0.25°) displayed on a grey background (black = 0.75 cd/m², white = 132 cd/m²). A fixation was presented at screen center on the first trial. A 10° target was presented immediately to one side of the fixation at random when participants fixated (Figure 3.1.1). The target was always aligned horizontally to the fixation. For subsequent trials, the fixation and target was presented in a random-walk pattern across the screen. The fixation appeared at a random location within 3° from the previous target position

Fixation duration was jittered ($M = 375$ ms, $SD = 125$) before the trial continued. Participants blinked or did not blink after fixation. For the blink condition, blink start was defined online as the moment the pupil area fell below 80% of the area at fixation. Blinks were then identified by the first eye sample where pupil area = 0 since blink start. Blink duration was very short ($M = 91.60$ ms, $SD = 74.52$). Fixation was extinguished at the next monitor refresh when pupil area was zero. There was no cue to signal the blink. Instead, the fixation and target were extinguished, and a warning message was shown whenever participants broke fixation before the full fixation duration. Such trials were then restarted.

Figure 3.1.1. Trial sequence for visually guided saccades (VGS), a) blink condition, b) no-blink condition, and memory guided saccades (MGS), c) blink condition and d) no-blink condition. VGS and MGS were randomized in each condition. The right eye was tracked, and viewing was binocular. A horizontal 10° target was presented randomly to one side of the fixation in a random-walk fashion. Participants fixated for a jittered duration of $375 \text{ ms} \pm 125$. Participants then blinked or remained fixated. The blink latency was 844.05 ms ($SD = 110.36$) for VGS and 852.37 ms ($SD = 108.05$) for MGS. The fixation was extinguished during the blink or after the trial-matched blink latency in no-blink condition. A saccade cue was heard 500 ms after fixation offset. Saccade latencies in blink condition for VGS and MGS were 298.84 ms ($SD = 60.11$) and 343.51 ms ($SD = 80.58$). Saccade latencies in no-blink condition for VGS and MGS were 268.01 ms ($SD = 64.38$) and 284.55 ms ($SD = 47.44$). The trial was terminated once the saccade ended. The inter-trial interval was 2000 ms. The following trial started within a 3° window from the previous target.

In the no-blink condition, the fixation was extinguished based on the trial-matched blink latency from the blink condition (i.e. the timepoint in which pupil area = 0 since blink start). Participants always began with a block of the blink condition before completing the no-blink condition. The blink latency was 844.05 ms ($SD = 110.36$) before VGS and 852.37 ms ($SD = 108.05$) before MGS. The trial was restarted if participants blinked during the fixation period.

Participants were cued to saccade to the target 500 ms after the fixation disappeared. The cue was an auditory beep (100 ms, 440 Hz, sinusoid). The target was either present (VGS) or absent (MGS) from the screen before the cue. VGS targets were extinguished after the saccade ended. The online detection for saccade end was indicated by velocity $< 30^\circ/\text{s}$ after the saccade started. MGS targets were extinguished together with the fixation. In the blink condition, targets and/or fixation were extinguished during the blink at the next monitor refresh. In the no-blink condition, targets and/or fixation were extinguished after the trial-matched blink latency. The next trial always began randomly within 3° of the previous target. Saccade latencies for VGS and MGS in the blink condition were 298.84 ms ($SD = 60.11$) and 343.51 ms ($SD = 80.58$), and latencies in the no-blink condition were 268.01 ms ($SD = 64.38$) and 284.55 ms ($SD = 47.44$) respectively.

3.1.3: Procedure

Viewing was binocular and the right eye was tracked. The eye tracker was calibrated using the 5-point procedure. Participants were instructed to maintain fixation and look quickly at the target after a beep. Participants knew they had to blink or abstain from blinking before the beep. They were also aware that the fixation sometimes disappears, and they had to remain fixated. All participants began with a block of the blink condition before completing a block of the no-blink condition.

A red fixation dot appears and turns white when participants fixate. The color change was to indicate which dot was the fixation because the target was presented simultaneously upon fixation. The target was presented horizontally to a random side of the fixation 10° apart. Participants sometimes made express/reactive saccades to the target. This was frequent at the start of the experiment. Some participants blinked early in the blink condition before the full fixation duration, or accidentally blinked in the no-blink condition during fixation. For such cases, a message “Fixate please!” appeared on the screen and the trial was restarted. Participants sometimes drifted while trying to maintain fixation (i.e. drift error $> 3^\circ$). The 5-point calibration was repeated for large drift errors and the trial was restarted.

Participants were instructed to remember the position of the target when fixating because the target might disappear. The fixation was extinguished during the blink or after the trial-matched blink latency for the no-blink condition. On half the trials, the target disappeared together with the fixation (MGS). The target stayed on for VGS. A three second limit from the end of fixation was imposed for the blink condition. “Blink please!” appeared on screen and the trial was restarted when participants did not blink within the allocated duration. In the no-blink condition, participants witnessed the fixation and/or target disappearing while waiting for the saccade cue.

Saccade cue was heard 500 ms after the fixation disappeared in both conditions. Participants looked quickly at the target (VGS) or the remembered location (MGS). A three second limit was enforced after the saccade cue. “Saccade please!” was shown if participants did not saccade within the time limit and the trial was restarted. The trial ended after the saccade. This was followed by a 2000 ms inter-trial interval. A new fixation dot was randomly presented around 3° of the previous target.

The message to fixate, blink, or saccade was always presented for three seconds. Both the fixation and target were extinguished before the message appeared. The trial was restarted after the message duration. There were 50 VGS and 50 MGS trials, fully randomized per block, in each condition. There were two blocks per condition. Participants completed two sessions over separate days. Each session comprised of one block of blink and no-blink condition, which lasted approximately 45 minutes including rest. Participants completed 400 trials in total (200 VGS and 200 MGS).

3.1.4: Gaze position analysis

Gaze position analysis were conducted offline in MATLAB (Mathworks Inc., Natick, MA, USA). Specifically, the horizontal and vertical gaze positions were computed offline. We evaluated fixation position by averaging gaze positions in a 100 ms window beginning from 500 ms before the fixation was extinguished. Fixation errors were obtained by subtracting the fixation coordinates from the averaged fixation position.

Saccade onset position was defined as the first instance five successive eye velocity samples exceeded the threshold ($> 30^\circ/\text{s}$). Saccade onset errors were defined as the distance between onset position and fixation position. Saccade end was identified when an average of 20 samples (20 ms) fell below the velocity threshold since onset. Saccade landing position was then quantified as the average gaze position lasting up to 50 ms after saccade ended. Landing errors were calculated by subtracting saccade end position from target position. We only analyzed primary saccades to the target beginning on/after the cue. Saccade amplitudes were calculated by subtracting saccade starting position from saccade landing position for horizontal and vertical directions. We also computed oblique saccade amplitudes because we expected

untrained participants to sometimes make slightly oblique saccades due to drifts or other biases.

Blink start was determined offline as the first sample where missing pupils (area = 0) persisted for more than 20 ms. Blink end was the last sample of missing pupils since blink start. Voluntary blinks at moderate strength has an approximate blink-related eye movement amplitude of 1° (Riggs et al., 1987). At this amplitude, the time taken for the eyelids to cover the eyes (i.e. down-phase) is ~30 ms. The eyelids take twice the time to return to their original position (Evinger et al., 1991). Based on this, we defined pre-blink as 30 ms before blink-start and post-blink as 60 ms after blink-end. We calculated pre-blink gaze position by averaging 100 ms of gaze positions before pre-blink, or until the gaze sample before fixation ended, whichever was earlier. Post-blink gaze position was the averaged gaze position, 100 ms after post-blink, or until the sample before the saccade started, whichever was earlier. We only analyzed pre-blink and post-blink positions for trials where no additional micro-saccades occurred between fixations, blinks, and saccades.

Leftward and rightward saccades were pooled since there are generally no differences (Collewyn et al., 1988a). This also bolstered statistical power. Errors were transformed such that positive values indicate forward (horizontal) or upward (vertical) gaze, while negative errors indicate backward (horizontal) or downward (vertical) gaze.

3.1.4.1: Fixation errors analysis

The following section describes how we defined fixation errors. The dot was extinguished during the blink. Thus, pre-blink and post-blink positions were called before-fixation-disappear and after-fixation-disappear positions. We computed the before-fixation-disappear and after-fixation-disappear positions in no-blink condition

from the same methods described above, using the fixation disappearance as reference. Before-fixation-disappear and after-fixation-disappear errors were derived by subtracting the fixation coordinates from the gaze positions.

3.1.4.2: Statistical analysis software and descriptive statistics

Statistical analyses and linear-mixed modelling were conducted on RStudio (2020). These packages were used in RStudio: *lmerTest* for modelling linear-mixed models (Kuznetsova, Brockhoff, & Christensen, 2015), *MASS* for stepwise regression (Venables & Ripley, 2013), *bayestestR* for computing Bayes factor and Bayes factor change across different models (Makowski, Ben-Shachar, & Lüdtke, 2019), and *ggplot2* for illustrating the figures (Wickham, 2016).

No prior studies exist which tested similar hypothesis or used the same paradigm. Instead risking an over- or under-inflation the expected power and effect sizes, this experiment used a Bayesian statistical analysis approach for evaluating the analysis. Bayes factor analysis compares the true effect as compared to the robust null. It does not inflate the chance of misleading evidence and reduces the chance of inconclusive evidence (Schönbrodt & Wagenmakers, 2018). We reported Bayes factor as *BF* in the remaining text. Larger *BF* values indicate lower rate of misleading evidence. This can be demonstrated using simulations. For instance, at power = .80, a simulated sample size of $N = 185$ is needed to produce a true effect, $BF > 5$. Alternatively, a simulated sample size of $N = 33$ can also achieve the same true effect, $BF > 5$, at the same power = .80 (Stefan, Gronau, Schönbrodt, & Wagenmakers, 2019). In general, $BF > 3$ indicates a true effect (Lazar, 2011). The larger the *BF*, the greater the effect observed at the population level.

Data from three participants were excluded from analysis because they failed to complete all conditions. This resulted in a total number of participants analyzed, N

= 10, $M = 26.70$ years old, $SD = 3.55$, 1 female. In the blink condition, trials were discarded if participants blinked more than once before the saccade cue. In the no-blink condition, trials were removed if participants blinked. Landing errors exceeding 3° were discarded. In total, we removed 856 (42.80%) MGS trials and 714 (35.70%) VGS trials in the blink condition, and 1031 (51.55%) MGS trials and 772 (38.60%) VGS trials in the no-blink condition. The large number of discarded trials were a result of inexperienced participants in eye tracking experiments.

According to the descriptive statistics, there were positive vertical amplitudes across some participants. This indicated that participants made oblique saccades. We examined whether amplitudes between oblique and horizontal saccades contrasted across blinks and saccade types. Since there were no differences between oblique and horizontal amplitudes, we reasoned that saccade landing errors could not be explained by oblique saccades. Additionally, the lack of differences suggested that we could infer amplitudes by looking at starting and landing errors. Therefore, we did not analyze amplitudes for the remaining analyses.

3.1.4.3: Linear mixed model to investigate blinks and saccade planning

The following analysis is exploratory to examine the influence of blinks on saccade planning. We used linear mixed models (LMMs) to test the influence of blinks on saccade planning. LMMs were conducted separately for horizontal and vertical landing errors as dependent variables. Fixed effects were the blink and no-blink conditions (Blinks) and saccade types (Type). Random effects were participant number, blink conditions, and saccade types. We investigated which model best predicted the saccade landing errors by excluding variables iteratively until the reduced model.

Full model: Landing error $\sim$ Blinks $\times$ Type + (1 | Ppt) + (1 | Blinks : Ppt) +
(1 | Type : Ppt)

Model 1: Landing error $\sim$ Blinks $\times$ Type + (1 | Ppt) + (1 | Blinks : Ppt)

Model 2: Landing error $\sim$ Blinks $\times$ Type + (1 | Ppt) + (1 | Type : Ppt)

Model 3: Landing error $\sim$ Blinks $\times$ Type + (1 | Blinks : Ppt)

Model 4: Landing error $\sim$ Blinks $\times$ Type + (1 | Type : Ppt)

Model 5: Landing error $\sim$ Blinks + (1 | Blinks : Ppt)

Model 6: Landing error $\sim$ Blinks + (1 | Type : Ppt)

Reduced model: Landing error $\sim$ Blinks + (1 | Ppt)

When fitting LMMs in R using the lmerTest package, the syntax (1 | variable) treats the variable as a random effect. Interaction between two random effects can be estimated with the syntax (1 | variable_A : variable_B). Interaction between two fixed effects is the product between the variables (variable_A $\times$ variable_B). We now explain the rationale behind the models.

In the full model, we predicted that saccade landing error was a linear combination between an interaction of the blink conditions and saccade types: Landing error $\sim$ Blinks $\times$ Type. This was because we hypothesized that saccade accuracy would be affected based on which saccades were made and whether participants blinked or not. We then included three random effects to account for information not measured by our experiment. Specifically, saccade accuracy was also dependent individual differences from the participant (1 | Ppt), and the participant's involvement in the blink conditions (1 | Blinks : Ppt) and saccade type (1 | Type : Ppt). The justification was that trials were randomized. Participants did not follow a specific sequence to blink or to make different saccades. Therefore, we estimated participants as a random effect to account randomness in relation to individual differences.

Variables from models 2 – 6 were then subsequently omitted or swapped because of the exploratory nature of the analysis. All models, including the reduced model explained below, treated blinks as a fixed effect since our hypothesis tested the contributions of blinking on saccade accuracy.

The purpose of the reduced model was to compare how much the saccade accuracy changes based on blinking alone. Model fits were assessed by comparing AIC (Akaike, 1973) and Bayes factor change (BF_{change}) from the selected model against the full model (see previous experiment). The final model reported had the lowest AIC and highest Bayes factor change (BF_{change}).

3.1.4.4: Before-saccade errors comparison and rationale

Fixation errors, before-fixation-disappear errors, after-fixation-disappear errors, and saccade starting errors were calculated by subtracting gaze from the fixation position. We termed these errors *before-saccade errors*. Stepwise regression tested the second hypothesis: do fixation errors predict saccade accuracy after a plan is created. However, before-saccade errors could differ between blinks and saccade types. If this happened, it would suggest that participants were not fixating before the saccade started. Therefore, it was an important step to establish no differences between before-saccade errors before running the stepwise regression.

We determined if before-saccade errors contrasted simultaneously across blinks and saccade types by running a 4x2 MANOVA using Pillai's trace statistic. The analysis was conducted separately for horizontal and vertical errors. We also ran univariate analyses for each before-saccade errors across conditions and saccade types. In general, before-saccade errors did not differ across blinks and saccade types.

3.1.4.5: Stepwise regression investigates fixation errors on saccade planning

The following was an exploratory analysis to evaluate which before-saccade errors could best predict saccade accuracies. We pooled each participant's before-saccade errors across blinks and saccade types to compute correlations between these errors. The purpose of the correlation was to assess if highly correlated variables should be included/excluded from the stepwise regression. As we shall see, stepwise regression excluded some highly correlated variables and improved the overall model fit. However, this did not always produce meaningful regression models. Variables were then manually excluded based on the correlations to attain a parsimonious model. We justified our decision to manually exclude variables if the final regression model have low AIC and high Bayes factor change values.

We tested the second hypothesis by investigating which before-saccade errors predicted landing errors. Stepwise regression was conducted on before-saccade errors before each participant's errors were pooled across blinks and saccade types. The full model was: Saccade landing errors ~ Fixation + before-fixation disappear errors + after-fixation-disappear errors + Onset errors + Blink condition + Saccade Type. Continuous predictors were before-saccade errors and categorical predictors were blink and saccade type. The stepwise regression was computed twice, once for horizontal landing errors, and once for vertical saccade landing errors. Model improvements during each regression step were evaluated by comparing the current adjusted R^2 , AIC, and Bayes factor change (BF_{change}) to the previous regression step.

3.1.4.6: Tracker drift and systematic bias analysis

Tracker drift or other systematic biases could influence before-saccade and landing errors. We conducted a time-course analysis to investigate the role of drift/biases on before-saccade and landing errors across blinks and saccade types.

Errors were visualized as a function of time for each participant. A best-fit line was fitted to the time-course for each error. The slope of the line quantified drift/bias. There was no sign of drift/bias if slope = 0 (i.e. flat line). We compared if the fitted slopes were statistically different from zero by running one-samples *t*-tests and computing the Bayes factor.

Results

3.1.5: Descriptive statistics for horizontal amplitudes and landing errors

Saccades undershot the target. Horizontal saccade amplitudes were larger for VGS ($M_{\text{Blink}} = 9.84^\circ$, $SD = .83$, $M_{\text{No-blink}} = 9.49^\circ$, $SD = .87$) than MGS ($M_{\text{Blink}} = 8.75^\circ$, $SD = 1.07$, $M_{\text{No-blink}} = 8.67^\circ$, $SD = 1.14$) in both conditions (Figure 3.1.2a). Horizontal amplitudes for VGS were greater if participants blinked, $t(9) = 4.08$, $SD = .26$, $p = .003$, $BF = 17.65$. There were no differences for horizontal MGS amplitudes across conditions, $t(9) = .89$, $SD = .37$, $p = .40$, $BF = .43$.

VGS was more accurate than MGS. Horizontal landing errors were smaller for VGS ($M_{\text{Blink}} = -.27^\circ$, $SD = .76$, $M_{\text{No-blink}} = -.54^\circ$, $SD = .86$) than MGS ($M_{\text{Blink}} = -1.22^\circ$, $SD = 1.01$, $M_{\text{No-blink}} = -1.24^\circ$, $SD = 1.12$) in both conditions (Figure 3.1.2b). Horizontal landing errors in VGS were statistically further away from the target when participants did not blink, $t(9) = 6.14$, $SD = .13$, $p = .0002$, $BF = 180.85$. There were no differences for MGS, $t(9) = .36$, $SD = .36$, $p = .73$, $BF = .33$.

3.1.5.1: Descriptive statistics for vertical amplitudes and landing errors

Vertical amplitudes were positive. Vertical amplitudes did not deviate much from the target's horizontal plane for VGS ($M_{\text{Blink}} = -.02^\circ$, $SD = .47$, $M_{\text{No-blink}} = -.10^\circ$, $SD = .42$) or MGS ($M_{\text{Blink}} = -.04^\circ$, $SD = .44$, $M_{\text{No-blink}} = -.12^\circ$, $SD = .44$) in both conditions (Figure 3.1.2c). Vertical amplitudes were larger for VGS when participants

did not blink, $t(9) = -2.30$, $SD = .13$, $p = .047$, $BF = 1.85$. However, this difference was absent in MGS, $t(9) = -1.96$, $SD = .14$, $p = .08$, $BF = 1.23$.

Figure 3.1.2. Saccade amplitude and landing errors. a & b) horizontal, c & d) vertical, and e) oblique direction. VGS: visually guided saccade, MGS: memory guided saccade. Dashed line in a) indicates target size. Each symbol represents average amplitude/landing error from the same participant ($N = 10$).

Vertical landing errors did not stray far from the vertical target position for VGS ($M_{\text{Blink}} = -.21^\circ$, $SD = .75$, $M_{\text{No-blink}} = -.20^\circ$, $SD = .69$) and MGS ($M_{\text{Blink}} = -.17^\circ$,

SD = .80, $M_{\text{No-blink}} = -.15^\circ$, SD = .79) across conditions (Figure 3.1.2d). There were no differences for vertical offset errors in VGS, $t(9) = -.47$, SD = .23, $p = .65$, $BF = .34$, or in MGS, $t(9) = -.21$, SD = .28, $p = .84$, $BF = .31$.

3.1.5.2: Descriptive statistics for oblique amplitudes and summary

Oblique saccade amplitudes were larger for VGS ($M_{\text{Blink}} = 9.85^\circ$, SD = .83, $M_{\text{No-blink}} = 9.50^\circ$, SD = .87) than MGS ($M_{\text{Blink}} = 8.76^\circ$, SD = 1.07, $M_{\text{No-blink}} = 8.68^\circ$, SD = 1.15) in both conditions (Figure 3.1.2e). The average oblique amplitudes were $.01^\circ$ larger than horizontal amplitudes across blinks and saccade types, but not statistically different, $F(1, 63) = .035$, $p = .85$, $BF = .23$. Since there were no differences between oblique and horizontal amplitudes, we could infer horizontal amplitudes from horizontal landing errors. Hence, we did not analyze amplitudes in subsequent analyses.

In summary, saccades undershot the targets horizontally and landed lower than the target. VGS was more accurate than MGS. Although the average oblique saccade amplitude was $.01^\circ$ larger than horizontal amplitude, the difference was insignificant. Hence, we concluded that horizontal amplitudes could be inferred from horizontal starting and landing errors. We investigated landing errors for the remaining analyses.

3.1.5.3: LMM estimating landing errors

We tested the influence of blinks on saccade planning using LMM. We first estimated horizontal landing errors. The best model in predicting horizontal landing errors was the full model (Table 3.1.1). The evidence from the full model was large as compared to an intercept-only model ($BF_{\text{Change}} = 2.91 \times 10^{8711}$).

According to the model, blinking alone did not influence horizontal landing errors across VGS and MGS ($p = .61$). On average, VGS were 0.93° larger than MGS ($p = 1.54 \times 10^{-5}$). The interaction term was significant, $p = 1.72 \times 10^{-4}$, indicating that

errors were -0.20° more backward for VGS in the no-blink condition (Figure 3.1.3).

The full model had a smaller AIC than the reduced model ($AIC_{Full} = 12111.50$, $AIC_{Reduced} = 13194.76$), and contributed greatly to the DV over the reduced model ($BF_{Change} = 4.30 \times 10^{229}$).

Figure 3.1.3. Horizontal landing errors interaction effect. Error bars depict SEM.

The LMM was repeated for vertical landing errors (Table 3.1.2). The full model did not predict vertical landing errors as well as an intercept-only model, $BF = .002$. Model 5 was better at explaining vertical landing errors than an intercept-only model, $BF = .02$. Although the final model was better at capturing vertical landing errors over model 5 ($BF_{Change} = 1.9$), model 5 was more parsimonious. Therefore, the final model was model 5. According to the model, vertical landing errors did not differ whether participants blinked or not ($p = .91$).

In summary, blinking alone did not influence horizontal landing errors across both saccades. However, blinking significantly improved VGS accuracy as compared to not blinking before VGS. There were no differences for vertical landing errors.

Table 3.1.1. LMM statistics for horizontal landing errors.

	Estimate	SE	<i>t</i> -Value	<i>p</i>
Intercept	-1.22°	.11	-11.21	4.63×10^{-10}
Blinks (No-blink)	-.04°	.07	-.52	.61
Type (VGS)	.93°	.12	7.80	1.54×10^{-5}
Blinks (No-blink) $\times$ Type (VGS)	-.20°	.05	-3.76	1.72×10^{-4}
Variance Component		SD		
Blinks : Participants		.14		
Type : Participants		.25		
Participants		.16		
Residual		.89		
Model comparison				
(Model vs. Full)	BF_{change}			
Model 1	1.02×10^{-31}			
Model 2	1.10×10^{-5}			
Model 3	3.72×10^{-32}			
Model 4	4.05×10^{-4}			
Model 5	1.01×10^{-228}			
Model 6	1.01×10^{-6}			
Empty	2.32×10^{-230}			

Table 3.1.2. LMM statistics for vertical landing errors.

	Estimate	SE	<i>t</i> -Value	<i>p</i>
Intercept	-.17°	.18	-.91	.38
Blinks (No-blink)	.03°	.26	.11	.91
Variance Component		SD		
Blinks : Participants		.58		
Residual		.53		
Model comparison (Model vs. Full)	<i>BF</i> _{change}			
Model 1	3.50×10^{-5}			
Model 2	3.72×10^{-35}			
Model 3	1.02×10^{-6}			
Model 4	3.51×10^{-39}			
Model 5	.53			
Model 6	3.14×10^{-34}			
Empty	2.26×10^{-34}			

3.1.5.4: Before-saccade errors

From the descriptive statistics, horizontal before-saccade errors were more forward from the horizontal fixation position (Figure 3.1.4a, c, e, and g). Vertical before-saccade errors were below the vertical fixation position (Figure 3.1.4, d, f, and h). We then determined if before-saccade errors differed concurrently across conditions and saccade types, in preparation for the stepwise regression.

Figure 3.1.4. Before-saccade errors across blinks and saccade types. a,c,e,g) Horizontal errors, and b,d,f,h) vertical errors. Symbols indicate average error for each participant.

Before data across different before-saccade errors could be pooled for stepwise regression, we must ensure that there were no differences between the errors. This would indicate that participants were indeed fixating. The 4x2 MANOVA found no simultaneous differences for horizontal and vertical before-saccade errors across blinks and saccade types. Horizontal before-saccade errors did not differ for blinks, $F(1, 4) = 2.58, p = .06$, Pillai's trace = .24, $\eta_p^2 = .24$, or saccade types, $F(4, 33) = 2.28, p = .08$, Pillai's trace = .22, $\eta_p^2 = .22$, and the interaction was not significant, $F(4, 33) = .05, p = .99$, Pillai's trace = .006, $\eta_p^2 = .006$. Vertical before-saccade errors did not differ for blinks, $F(4, 33) = 1.21, p = .33$, Pillai's trace = .13, $\eta_p^2 = .13$, or saccade types, $F(4, 33) = .14, p = .97$, Pillai's trace = .02, $\eta_p^2 = .02$, and the interaction was not significant, $F(4, 33) = .23, p = .92$, Pillai's trace = .03, $\eta_p^2 = .03$.

Univariate analyses for each horizontal before-saccade errors exhibited no differences across blinks and saccade types except for start errors. Start errors were more forward for MGS than VGS, $F(1, 36) = 7.14, p = .01, \eta_p^2 = .05, BF = 4.61$, but not for blinks, $F(1, 36) = 1.92, p = .17, \eta_p^2 = .17, BF = .60$. The interaction was not significant, $F(1, 36) = .03, p = .86, \eta_p^2 = .001, BF = 1.17$. Univariable analyses for each vertical before-saccade errors showed no differences across blinks and saccade types ($p > .05$). Although start errors were more forward for MGS than VGS, this difference was not related to the blink. There could be tracker drifts or other systematic biases which led to this difference. However, in a later analysis (see 3.1.5.6), we found no evidence of tracker drifts and systematic biases. Thus, we reasoned that this was enough information to pool before-saccade errors.

We pooled before-saccade errors across blinks and saccade types for each participants (Figure 3.1.5) and compared the pooled data. Horizontal errors were statistically different from each other, $F(3, 36) = 25.83, p = 4.32 \times 10^{-9}, \eta_p^2 = .68, BF =$

2.25×10^6 (Figure 3.1.5a). Post-hoc analysis using Bonferroni correction revealed that onset errors were larger than fixation errors ($M_2 - M_1 = .27^\circ$, $p = 4.00 \times 10^{-8}$), before-fixation disappear errors ($M_2 - M_1 = .27^\circ$, $p = 4.70 \times 10^{-8}$), and after-fixation disappear errors ($M_2 - M_1 = .23^\circ$, $p = 1.90 \times 10^{-6}$). Vertical before-saccade errors did not differ from each other, $F(3, 27) = 1.02$, $p = .40$, $BF = .13$ (Figure 3.1.5b).

Figure 3.1.5. Average before-saccade errors and correlation matrix for a & c) horizontal errors, and b & d) vertical errors. *** $p < .001$, ** $p < .01$, * $p < .05$. Errors were pooled across blinks and saccade types to compute the correlation matrix. Colored dots in a) and b) reflect average errors per participant. Horizontal errors were highly correlated for Fixation and before-fixation disappear errors, and for after-fixation disappear errors and saccade starting errors. Horizontal before-fixation disappear errors and after-fixation disappear errors were moderately correlated. This indicates that the eyes were slowly moving towards the target, but at a pace not quick enough for saccade detection. All vertical before-saccade errors were highly correlated to each other. This suggests that vertical errors remain stable throughout the experiment. Correlations were used to evaluate if variables included/excluded from the subsequent stepwise regression were meaningful.

The correlation matrix was calculated using the pooled before-saccade errors in each direction. The purpose of the correlation matrix was to check if the following

stepwise regression analysis included/excluded variables meaningfully. Some horizontal errors were correlated (Figure 3.1.5c). Fixation errors and before-fixation disappear errors were highly correlated ($p < .001$), before-fixation disappear errors and after-fixation disappear errors were moderately correlated ($p < .05$), after-fixation disappear errors and saccade starting errors were moderately correlated ($p < .001$). All vertical errors were highly correlated (Figure 3.1.5d).

In summary, horizontal and vertical before-saccade errors did not simultaneously differ across blinks and saccade types. Horizontal start errors were more forward for MGS than VGS, indicating that MGS started closer to the target than VGS. Some horizontal errors were correlated: Fixation and before-fixation disappear, before-fixation disappear and after-fixation disappear, and after-fixation disappear and saccade starting errors. This implied that the eyes were slowly moving towards the target. However, the movement was not fast enough to trigger a saccade detection. All vertical errors were correlated. This signified that vertical errors remained stable throughout the experiment. Highly correlated variables should predict saccades in the following stepwise regression. However, this was not the case. Some highly correlated variables were excluded because they did not predict saccades adequately.

3.1.5.5: Stepwise regression evaluates which before-saccade errors predicted saccade landing errors

Stepwise regression was conducted to determine which before-saccade errors predicted landing errors. We first ran regression on horizontal landing errors (Table 3.1.3). The analysis indicated that landing errors were best predicted by fixation errors, after-fixation disappear errors, saccade starting errors, and saccade type, $F(4, 35) = 20.74$, $S.E. = .31$, $p = 7.75 \times 10^{-9}$, adjusted $R^2 = .67$. This model explained 67% of horizontal landing errors. When compared to the full model, this model made

moderate contributions in explaining landing errors ($BF_{\text{Change}} = 15.46$). However, the estimate for fixation was not significant.

We ran an additional step by excluding fixation as a continuous predictor $F(3, 36) = 26.27$, $S.E. = .32$, $p = 3.51 \times 10^{-9}$, adjusted $R^2 = .66$. This model explained 66% of the variance for landing errors. When compared to the full model, this model made moderate contributions in explaining landing errors ($BF_{\text{Change}} = 32.4$). The Bayes factor change over the full model was larger than the model suggested by stepwise regression. Hence, the final model was: Landing error $\sim 1.74^{\circ}_{\text{After-fixation-disappear}} - 1.03^{\circ}_{\text{Saccade starting}} + .77^{\circ}_{\text{VGS}} - 1.04^{\circ}$ (Table 3.1.3).

Saccade type was a better predictor for horizontal landing errors than before-saccade errors. The model with all before-saccade errors and no saccade type predictors only explained 18% of the variance for landing errors. In addition, the model did not contribute to the evidence over the final model ($BF_{\text{Change}} = 6.66 \times 10^{-9}$).

Vertical landing errors were predicted by fixation errors, $F(1, 38) = 469.60$, $S.E. = .15$, $p = 2.20 \times 10^{-16}$, adjusted $R^2 = .92$ (Table 3.1.4). The final model was: Landing errors $\sim 1.31^{\circ}_{\text{Fixation error}} + .13^{\circ}$. This model explained 92% of the variance for vertical landing errors. When compared to the full model, the final model made large contributions in explaining landing errors ($BF_{\text{Change}} = 689.95$). The other models rejected by the stepwise regression also explained 92% of the variance for vertical landing errors. However, these models did not predict vertical landing errors as well as the final model. The Bayes change for each step of the regression over the full model was not as large as the final model: five predictors ($BF_{\text{Change}} = 5.08$), four predictors ($BF_{\text{Change}} = 22.01$), three predictors ($BF_{\text{Change}} = 76.09$), and two predictors ($BF_{\text{Change}} = 247.72$). Hence, the final model was the most parsimonious model.

Table 3.1.3. Stepwise regression on horizontal landing errors.

Predictors	Adjusted R^2	R^2 Change	F	AIC Change	BF Change	p
Fixation, Before-fixation disappear, After-fixation disappear, Saccade starting, Blinks, Type	.67	-	13.94	29.77	-	7.80×10^{-8}
Fixation, Before-fixation disappear, After-fixation disappear, Saccade starting, Type	.68	.01	17.23	-1.99	6.28	1.76×10^{-8}
Fixation, After-fixation disappear, Saccade starting, Type	.67	-.01	20.74	-.11	2.46	7.75×10^{-9}
After-fixation disappear, Saccade starting, Type	.66	-.01	26.27	-.21	2.1	3.51×10^{-9}
Saccade starting, Type	.58	-.08	28.33	7.24	.06	3.45×10^{-8}
Fixation, Before-fixation disappear, After-fixation disappear, Saccade starting	.18	-.40	3.19	28.72	1.07×10^{-7}	.02
Final Model	Estimate	S.E	t	p		
(Intercept)	-1.04°	.15	-7.08	2.58×10^{-8}		
After-fixation disappear	1.74°	.57	3.06	.004		
Saccade starting	-1.03°	.39	-2.66	.01		
Type (VGS)	.77°	.11	7.00	3.25×10^{-8}		

Table 3.1.4. Stepwise regression on vertical landing errors.

Predictors	Adjusted R^2	R^2 Change	F	AIC Change	BF Change	p
Fixation, Before-fixation disappear, After-fixation disappear, Saccade starting, Blinks, Type	.92	-	78.53	-27.17	-	2.2×10^{-16}
Fixation, After-fixation disappear, Saccade starting, Blinks, Type	.92	.001	95.97	-1.56	5.08	2.2×10^{-16}
Fixation, After-fixation disappear, Saccade starting, Blinks	.92	.0008	121.00	-1.24	4.33	2.2×10^{-16}
Fixation, Saccade starting, Blinks	.92	.0004	160.70	-.79	3.46	2.2×10^{-16}
Fixation, Saccade starting	.92	.0004	239.00	.67	3.26	2.2×10^{-16}
Fixation	.92	-.001	469.60	-.36	2.79	2.2×10^{-16}
Final Model	Estimate	S.E	t	p		
(Intercept)	.13°	.03	4.65	3.89×10^{-5}		
Fixation	1.31°	.06	21.67	2.00×10^{-6}		

In summary, horizontal landing errors were predicted by after-fixation disappear errors, saccade starting errors, and saccade type. Blinking did not contribute to, nor did it improve model fits. This meant that events after the fixation disappeared were better at explaining saccade accuracy. Additionally, saccade type was a strong predictor for horizontal saccade accuracy. Consequently, this suggests that the saccade plan is updated close to an impending saccade. Vertical landing errors were predicted by fixation. This suggests that vertical errors remain stable throughout the experiment. Therefore, some fixation errors predicted saccade accuracy.

3.1.5.6: Time-course analysis

We analyzed the time-course to ensure that the results were not attributed to tracker drift or other systematic biases. Drift/bias was quantified by the slope of a best-fit line when errors were plotted as a function of time (Figure 3.1.6). Slopes from the time-course plots were visualized separately across conditions and saccade types (Figure 3.1.7). Our results showed no evidence of drift/bias (Figure 3.1.8). Slopes were not significantly greater than zero for both horizontal and vertical errors ($p > .05$, $BF < 3$). In short, there were no evidence of drift/bias because the best-fit slopes were not statistically different from zero (i.e. slope = 0 signified no drift/bias).

Figure 3.1.6. Horizontal fixation errors as a function of time. MGS: memory-guided saccades, VGS: visually-guided saccades. Colors indicated individual observations per participant. The slope from the best-fit line denoted tracker drift.

Figure 3.1.7. Slopes from time-course analysis. MGS: memory-guided saccades, VGS: visually-guided saccades. Symbols indicate individual slopes.

Figure 3.1.8. Time-course significance values from one-sample t -tests. Significant values were colored in blue and gold. The tests did not reveal evidence of tracker drift or other systematic biases.

Discussion

3.1.6: Saccade plan updates after the blink and saccade accuracy is predicted by events after blinking

We plan saccades to direct our eyes when exploring the visual environment. However, we do not make saccades alone when exploring; we also blink. In this experiment, we tested whether saccade plans were updated by blinking. Participants blinked or remained fixated before making visually-guided or memory-guided (VGS/MGS) saccades to 10° horizontal targets across the screen.

We analyzed saccade accuracy and found some evidence of saccade updating in VGS. Saccades were more accurate when participants blinked. This was not the same for MGS. Blinking did not influence MGS accuracy. Saccades started and ended lower than the vertical target position. This was not influenced by blinking or saccade types and was relatively stable throughout the experiment.

In general, before-saccade errors did not differ across conditions or saccade types. Although MGS started closer to the target than VGS, MGS also undershot the target more than VGS. We then investigated which before-saccade errors predicted the saccade. We found that horizontal accuracies were predicted by after-fixation disappear errors, saccade starting errors, and saccade type, suggesting that the events near the upcoming saccade predicted saccade accuracy. Vertical accuracies were predicted by fixation errors, signifying that vertical errors remained stable throughout the experiment. Therefore, our results showed that some fixation errors predicted the upcoming saccade.

We also conducted a time-course analysis to determine if our results were due to tracker drift or systematic biases. Errors were visualized across time and a best-fit line was fitted to obtain the slope coefficient. The coefficient quantified tracker drift and/or biases. We ran one-samples *t*-tests and Bayes factor analyses on the slopes and found no statistical differences. This indicated that errors did not change systematically over the course of the experiment, arguing against the notion that our results were attributed to tracker drift or systematic biases.

3.1.6.1: Saccade planning and blinking

The planned saccade directs our gaze towards a goal so that we can coordinate subsequent movement or action (Hayhoe, Shrivastava, Mruczek, & Pelz, 2003). Saccade plans are cancelled and re-programmed when the goal changes unexpectedly (Ray et al., 2004; Vergilino-Perez & Beauvillain, 2004). The updated plan directs the eyes to the goal position regardless of the initial eye position (Vergilino & Beauvillain, 2000).

We found evidence that blinking updates saccade plans for horizontal saccades (Figure 3.1.2a & b). The linear mixed models revealed significant interaction between

blink and saccade type for horizontal landing errors (Table 3.1.1 and Figure 3.1.3). Specifically, horizontal landing errors were smaller for blink MGS than no-blink VGS ($p = .0002$, $BF = 180.85$). This was not explained by different starting errors between blink conditions since saccade starting errors were not statistically different. Saccade starting errors were significantly different for saccade types. MGS started closer to the target than VGS (Figure 3.1.4g). Our results showed that saccade plans for a single saccade were updated simply by blinking ~500 ms before the saccade.

We speculated that blinks may influence vertical MGS because they are both controlled by the inferior rectus muscles (Evinger, Shaw, Peck, Manning, & Baker, 1984; Metz, 1980). Vertical MGS should be more accurate if the plan was updated by the blink. However, we found no differences in vertical landing errors across blinks and saccade types. It was possible there was no updating in MGS since MGS become less accurate over time (Ohtsuka et al., 1989). Alternatively, target absence could imply a lack of updating since saccades are updated based on the eye distance to the target (Vergilino & Beauvillain, 2000). Unfortunately, our current paradigm could not address the role of saccade updating in vertical MGS since we only tested horizontal targets.

The way targets are encoded in memory could also explain the lack of differences in horizontal MGS. Vergilino and Beauvillain (2001) conducted a double-step saccade paradigm in which participants had to execute a VGS before the MGS to words of varying lengths. They showed that fixation errors at the end of the VGS was uncorrected before the MGS. They also demonstrated that, regardless of where the MGS started, saccades landed in the middle of the second word. This signified that memorized targets were encoded based on where the targets appeared with respect to the head position.

In our experiment, blinking did not influence the head-centric encoding of the target. Participant rested their head on the chin rest. It was likely MGS targets were encoded the same way regardless of the blink because the head position did not change. Hence, we found no differences for MGS accuracies. Future experiments could investigate the extent MGS accuracies are affected by blinking when the head position changes during saccade planning.

3.1.6.2: Blinking and saccade landing errors

Saccade landing errors may be enlarged by dynamic overshoots. Dynamic overshoots have small amplitudes ($< 1.5^\circ$) and are infrequent (Kapoula, Robinson, & Hain, 1986). Saccades without blinks can produce dynamic overshoots at the end of the saccade (Bahill, Clark, & Stark, 1975a). Dynamic overshoots can also occur when an observer blinks towards the end of the saccade (Hain, Zee, & Mordes, 1986; Peli & McCormack, 1986; Rottach et al., 1998). We tend to blink after large saccades because large horizontal saccades ($> 33^\circ$) activates the orbicularis oculi muscles which controls downward lid movements (Evinger et al., 1994).

It is unlikely dynamic overshoots are associated to orbicularis oculi muscle activations. There is no relationship between vertical saccade magnitude and orbicularis oculi muscle activation (Wouters et al., 1995). Rather, dynamic overshoots are likely associated to the lag when the omnipause neurons activate to cease the saccade (Zee & Robinson, 1979). This is supported by evidence showing that dynamic overshoots were greatest for fastest saccades (Rottach et al., 1998). Since the omnipause neurons experience some latency before stopping the saccade, faster saccades would have greater overshoots.

In our experiment, saccades were more accurate for VGS when participants blinked. This result cannot be explained by saccade-induced overshoots because

saccades were more accurate when participants blinked. Additionally, we did not find any differences for MGS across the blink condition. Landing errors only contrasted in VGS between the blink conditions, which indicated that blinks played a role in saccade accuracy to visible targets.

Our results cannot be explained by blink-induced dynamic overshoots. Participants blinked ~500 ms before the saccade, instead of during or after the saccade. From the literature, muscles were activated for 67% of saccades to 17° targets (Evinger et al., 1994). Our 10° targets could not reliably elicit orbicularis oculi muscle activation for every saccade. Moreover, it is unlikely the orbicularis oculi muscle is associated with dynamic overshoots (Wouters et al., 1995).

Blinks affect saccade velocity/duration at any saccade amplitude (Rottach et al., 1998). Saccades to the same target decreases in velocity (or increases in duration) if the saccade was combined with the blink. Velocity decreases for horizontal and vertical saccades if the observer blinked ~100 ms before the saccade, but are unchanged if the blink happens after the saccade begins (Rambold et al., 2002). Our results cannot be explained by such relationships. Saccade amplitudes remain unchanged since blinking only alters velocity (or duration). Therefore, saccade accuracies cannot be explained by the change in saccade kinematics due to the blink.

3.1.6.3: Specific fixational errors are involved in saccade planning

The time between an intent to the saccade and saccade execution is no longer than 200 ms (Bruce & Goldberg, 1985). Saccade plans are updated no earlier than 150 ms before the saccade takes flight (Bellebaum et al., 2005). Target position is updated as early as 40 ms (Kosovicheva et al., 2014). In our experiment, both fixation and target were presented at the start of the trial. The blink latency was more than 500 ms. Participants had plenty of time to plan the saccade before blinking or before the

fixation disappeared. Despite the time, horizontal saccade landing errors were only predicted by events occurring after the fixation disappeared. Specifically, horizontal saccade landing errors were predicted by after-fixation disappear, saccade starting errors, and saccade types (Table 3.1.3).

It is possible that saccades were predicted by events occurring after the dot disappeared due to anticipation. Anticipatory saccades occur when there is a delay between the saccade and the saccade cue (Kalesnykas & Hallett, 1987). Neurons which prepare saccades show increased activity to predictable saccades because of anticipation (Dorris & Munoz, 1998). Saccades are anticipatory if saccade reaction time < 90 ms upon target presentation. Anticipatory saccades can move in the opposite direction as the target (B. Fischer et al., 1993). The number of anticipatory saccades increases when cue latency lengthens (B. Fischer & Weber, 1998; Weber, Dürr, & Fischer, 1998)

Our data did not show evidence for anticipation. Saccade latencies for VGS and MGS in the blink conditions exceed the typical anticipatory latency of < 90 ms (B. Fischer & Ramsperger, 1984). Moreover, before-fixation disappear errors and after-fixation disappear errors were less forward than fixation and saccade starting errors (Figure 3.1.5a). Our results did suggest that the eyes were slowly moving toward the target at sub-velocity threshold. This was because each before-saccade error was systematically correlated across the trial (i.e. Fixation errors and before-fixation disappear errors, before-fixation disappear errors and after-fixation disappear errors, after-fixation disappear errors and saccade starting errors).

The saccade plan is likely updated near the time to saccade. Stepwise regression indicated that horizontal landing errors were predicted by after-fixation disappear errors, saccade starting errors, and saccade type (Table 3.1.3). Saccade

starting errors alone was not enough to predict saccade landing errors. Although there was some correlation between before-fixation disappear errors and after-fixation disappear errors (Figure 3.1.5c), before-fixation disappear errors were excluded early in the regression. If saccade plan was updated before the fixation disappeared, then fixation error and before-fixation disappear errors would also predict saccade landing errors. The final model indicated that events (i.e. errors) leading up to the start of a saccade were updated and thus, predicted saccade landing errors.

Care must be exercised when interpreting saccade updating for vertical errors from our results. We showed that vertical landing errors were best predicted by fixation (Table 3.1.4). However, this does not denote the lack of saccade updating for vertical directions. This model showed that vertical errors from fixation were uncorrected and remained stable throughout the trial. Participants made horizontal saccades, but vertical errors arise because the oculomotor system cannot maintain zero-error saccades. Moreover, our experiment was not designed to measure vertical saccades. As such, it was possible vertical errors remained stable throughout the trial because there was no need for the oculomotor system to ensure the saccade was also accurate vertically. Further investigations involving vertical or oblique saccades would better elucidate saccade updating in vertical directions.

Our results cannot be explained by tracker drift or systematic biases (Figure 3.1.6–3.1.8). The slopes for errors across time were relatively flat across all before-saccade errors horizontally and vertically (Figure 3.1.7). These slopes were also not significantly different from zero (Figure 3.1.8). Hence, fixation errors predicted saccade landing accuracy, even when the saccade plan was already created, not because of drifts or systematic biases.

3.1.6.4: Saccade planning and the real world

Motor plans are updated to help us reach a goal should our initial movements change (Shima et al., 1996). Saccade plans, like motor plans, direct the eyes to the goal. Saccade plans are also updated when the target changes unexpectedly (Vergilino & Beauvillain, 2000), so that our eyes land on the target. Our results show that saccade plans are updated when we blink ~500 ms before the saccade.

We explore the visual world by making saccades. We plan a saccade to look at an object. When we explore, we also sometimes blink. Blinking produces additional uncontrollable eye movements. If the saccade plan is not updated before the saccade, then our eyes may not land on the target since the eyes do not return to the exact position after each blink. The additional movements produced during the blink would also produce erroneous movement signals in the oculomotor system.

Saccade updating could be an oculomotor behavior that helps maintain perceptual continuity during visual exploration. When we want to look at a specific target, but we blink before looking, the oculomotor system updates the saccade plan to ensure that our eyes arrive at the target. The actual eye movement matches our intended movement and reaches the goal. This allows visual exploration to make sense because our eyes are directed to where we intent it to go.

3.1.6.5: Interim summary

We plan saccades when directing our eyes to look at objects or locations. We investigated whether these plans were updated when we blink. Saccades landed more accurately when participants blinked ~500 ms before saccades to visual targets. There were no differences for memory targets. This indicated that saccade plans were updated when participants blinked before the saccade started. Horizontal saccade accuracies were predicted by errors after the fixation disappeared. This implied that

saccade plans were updated near an impending saccade. However, vertical errors which were unimportant to the task remained stable throughout the experiment. Thus, our oculomotor system updates saccade plans to guide our eyes closer to where we want the look even when we blink.

General discussion for part 3

3.2.0: There is a signal which anticipates eye positions after blinking

Part 2 showed that temporal stability in vision is achieved by recruiting the oculomotor system to ensure stability. Specifically, the oculomotor system corrected gaze positions following endogenous disruptions to an object's position. The observation that the oculomotor system corrected for changes happening in the physical world implicated the presence of a signal which estimated the eye positions after blinking to aid in the correction.

The visual system processes visual samples between each saccade. However, we do not perceive the world as disjointed (Rolfs, 2015). This meant that temporal stability was achieved across the saccade because the perceptual system, after weighing visual information, considered the previous and current information to be contiguous. From part 2, we saw the role of the oculomotor system in maintaining perceptual continuity across the blink. This could be possible due to a signal which anticipated eye positions after blinking. The oculomotor system is also engaged for saccades. In other words, blinks and saccades are different arms of the oculomotor system. Therefore, we asked if this a signal which projected eye positions after blinking could also influence saccades.

We confirmed our speculation that this signal also influenced saccades by investigating saccade plan updating. Saccade plans tell the oculomotor system where to direct our eyes. If the plan is incorrect, then the eyes may never arrive at the correct location. Updating ensures that the saccade plan always receives the latest information so that the saccade remains accurate. When the observer blinked after making the saccade plan, saccades to visible targets became more accurate. This was in comparison to the observer maintaining fixation, and then making a saccade after an

interval. We confirmed our speculation because saccade plans were updated. The signal which anticipated eye positions after blinking was communicating within the oculomotor system, and the result was saccade plan updating. Hence, we concluded that there is a signal which anticipated eye positions after blinking, and that this signal could be used to ensure temporal stability by updating saccade plans.

3.2.1: The signal after blinking which updates saccade plans in relation to existing perspectives

Our understanding of temporal stability is extended to the following: temporal stability in vision is reached by the oculomotor system because there is a signal which anticipated eye positions after blinking. The oculomotor system can correct for positional changes of an object after blinking using this signal. The oculomotor system also uses this signal for saccade plan updating to ensure that our eyes land onto the target. However, this signal is only half the reason for maintaining perceptual continuity in vision.

Temporal stability in vision is achieved when the oculomotor system corrects the gaze or updates saccade plans. However, temporal stability in vision reached by the oculomotor system must not be isolated from other effects that also maintain some aspects of perceptual continuity. Specifically, we argue that temporal stability in vision is achieved by the oculomotor system because of a) the signal which anticipates eye positions after blinking, and b) contributions of other effects that also maintain parts of perceptual continuity. The following is a speculation which describes the interactions between hysteresis, object updating, and temporal stability in the oculomotor system and higher-order visual systems to illustrate this reasoning.

Hysteresis occur during saccade plan updating. When an observer blinks before making the saccade, a signal which projects the eye position is created in the

oculomotor system. This signal is communicated between the blink-associated and the saccade-associated arm of the oculomotor system. This signal could also be subjected to hysteresis before the saccade is launched. Hysteresis of this signal then serves as an anchor for the oculomotor system to re-assess how much modification is required to update the saccade plan, based on the amount of endogenous disruption introduced by the blink. Meanwhile, hysteresis carries visual information from the early visual cortices to the lateral occipital complex to create target representations. Object updating then occurs and the percept of the target is constantly sampled. The oculomotor system then launches the saccade and visual processing takes place at the end of the saccade. Since the target representation already exists, the perceptual system easily evaluates the newly sampled representation after the saccade to the representation from before the saccade. There is temporal stability when there is no difference between information.

In summary, there is a signal which anticipates eye positions after blinking. Saccade plans are updated thanks to this signal. As a result, our eyes land where we want even after blinking. Therefore, temporal stability in vision is successful because the oculomotor system uses this signal to update the saccade plan. Based on speculation, this signal, or the oculomotor system, could be subjected to hysteresis when updating saccade plans. Importantly, other effects which maintain some form of perceptual continuity may also play a role in temporal stability.

Part 3 conclusion

Part 3 asked if our speculation were true, that a signal was created to predict the eye positions after blinking, and that this signal would also affect saccades. This was motivated by the observations that the visual world does not appear discontinuous after blinking or making saccades. Since the oculomotor system is involved with

processing both blinks and saccades, and that blinks share similarities with saccades, this implicated that the signal generated by blinking could interfere with saccades.

We confirmed our speculation by testing saccade planning. Saccades are planned movements. When we blink, the eyes do not return to the identical position. When an observer blinks before a saccade, the start position after the blink would not coincide with those before the blink. Thus, the saccade would not be accurate if the oculomotor system relied on the old saccade plan. We showed that blinking after saccade planning resulted in saccade plan updating. Saccades to visible targets were more accurate when the observer blinked after planning the saccade, as compared to not blinking. The oculomotor system updated the saccade plans to guide our eyes closer to where we want the look even when we blink. Therefore, we reasoned that saccade plan updating enabled a continuous experience of visual exploration because our eyes land where we want them to.

The understanding of temporal stability was enhanced by the findings in part 3. Temporal stability in vision, achieved by the oculomotor system, was thanks to a signal which predicted eye positions after blinking. This signal helps to re-orient gaze after blinking and to update saccade plans. We speculated that effects from other perspectives of perceptual continuity could also contribute to temporal stability. In conclusion, we argued that temporal stability in vision is achieved because the oculomotor system uses a signal, created by blinking, to re-orient gaze and to update saccade plans. Furthermore, temporal stability could also be maintained by other effects involved in perceptual continuity.

General discussion for thesis

4.1: Temporal stability based on this thesis

This thesis extended the current understanding of temporal stability. In part 1, we provided evidence to show that temporal stability could be modality-specific. Specifically, through serial dependence, previous visual information continued to bias current visual responses. In part 2, we demonstrated that temporal stability was not simply a failure of change detection because the oculomotor system was recruited to maintain continuity during endogenous disruptions. Evidence from blink adaptation explicitly showed gaze correction towards positional changes of an object in the physical world. We speculated that the reason the oculomotor system could re-orient the gaze was due to a signal created by blinking. This signal anticipates eye positions after blinking. In part 3, our understanding of temporal stability was expanded because we confirmed our speculation in part 2. The evidence came from saccade plan updating, where blinking after constructing a saccade plan led to more accurate saccades. This indicated that the signal created when blinking led to saccade plan updating. We then speculated that other effects which maintain some aspects of perceptual continuity could also be part of temporal stability. Hence, according to the thesis, temporal stability can be expressed by serial effects in the case of serial dependence. In vision, temporal stability is not merely a failure of change detection because the oculomotor system is recruited to maintain perceptual continuity. This is possible because a signal is created whenever endogenous disruptions due to the blink occur. The oculomotor system uses this signal to re-orient our eyes either after blinking or to ensure our eyes land accurately at the target. Other effects, such as hysteresis and object updating, which contribute to perceptual continuity could also be contributing to temporal stability.

The definition of temporal stability, underlined by the thesis, is a better explanation than a catch-all definition from the existing literature. Instead of a mechanism which simply compares information, our explanation included specificity by showing that temporal stability could be modality-specific when expressed through serial dependence. We also provided evidence demonstrating how continuity was maintained during endogenous disruptions. Specifically, the oculomotor system uses a signal which anticipates eye positions to re-position the gaze or to ensure saccades are accurate by updating saccade plans. Our explanation also addressed the lack of considerations between various existing perspectives of perceptual continuity. We speculated how temporal stability could be reached by incorporating existing perspectives. Therefore, this thesis well addressed the current inadequate definition of temporal stability from the literature.

4.2: Shortcomings of this thesis and suggestions

The major failings of the definition of temporal stability postulated by the thesis is a result of the testing paradigms. Psychophysical paradigms were employed across all three parts of this thesis. As such, there was a heavy emphasis on behavioral outcomes of temporal stability. This was exemplified by parts 2 and 3 of the thesis which restricted investigations to the oculomotor system (i.e. gaze positions after blinking and saccade accuracy). As discussed in parts 2 and 3, there is a high degree of complexity across the brain involved in planning and eliciting blinks and saccades. The absence of other testing methods, such as neural data or brain imaging, limited how much the thesis' postulation held true. For instance, current perspectives of hysteresis utilized evidence using cortical activity in the lateral occipital complex to argue that object representations take place at higher-order visual processing areas (Ferber et al., 2005). It would be beneficial for future studies to show evidence of

temporal stability using neural data to bolster and support the definition held by this thesis.

Temporal stability may not entirely be modality specific as defined by the thesis. This would only address temporal stability when it is measured in the form of serial dependence. Perception is multisensory because the physical environment is multisensory. There are also brain regions that manage multimodal signals (J. Driver & Noesselt, 2008). Then again, although perception is multisensory, it is possible that some information remains predominantly unimodal during perceptual continuity. For instance, the perspective of continuity from object representations is based on visual information of a scene. From that perspective, object representations are visual. However, we can form non-visual object representations if we explore objects in the dark or with our eyes' closed by feeling the object. While we may not have information regarding visual features such as the object's color, we certainly can guess the shape, texture, and the size of the object. It may be premature to argue that temporal stability is modality-specific. Nevertheless, this does not mean that what this thesis postulated is useless. Rather, the added specificity that temporal stability is modality-specific serves as a steppingstone for subsequent research. Therefore, future studies could examine cross- or multimodal temporal stability to better enhance our understanding of it.

In relation to the previous point, can the oculomotor system maintain temporal stability in other ways? Congenital blind individuals are those who are born without sight from birth. Their visual cortices are severely atrophied because of the absence of visual stimulation (Ptito, Schneider, Paulson, & Kupers, 2008). However, some of these individuals use their visual cortex to *see* (Tinelli et al., 2013). This blindsight arises due to brain plasticity which allowed neuronal reorganizations in the visual

cortex, and cortical functions are changed (Tamietto & Morrone, 2016). Therefore, could plasticity modulate how the oculomotor system maintains temporal stability? If so, does this indicate that the oculomotor system would require a complex dynamic process which involves constant changes or updates to information to reach temporal stability? These are interesting questions which could be addressed in future studies.

4.3: What remains unanswered?

Temporal stability involves comparing information for perceptual continuity. However, the thesis has so far tested only low-level visual features like orientations (part 1) and spatial positions (parts 2 and 3). We still do not know what information is compared during the evaluation process. Is the information compared sensitive to individual features, such as color and contrast, or are more abstract forms of percepts compared such as object representations? Do they belong to one modality or are they multimodal? Once we understand the kind of information that is being compared, we would be able to answer whether temporal stability is truly modality-specific.

There is a lack of understanding in the interval that exists between the information during evaluation. We do not know when the evaluation process occurs, how immediate the information sampling is, nor how much time can pass before two identical sets of information are considered unstable or break continuity. Could temporal stability, like hysteresis, also be a part of memory? These are unfortunately difficult questions to answer by behavioral paradigms alone. We can only infer cortical processing at best using such paradigms. Therefore, more direct measurements on cortical activity should be exercised to answer these questions.

The definition for temporal stability proposed by this thesis involves investigating perceptual continuity during endogenous disruption caused by blinking. Is temporal stability achieved by exogenous disruptions caused by the environment? It

seems plausible that exogenous disruptions do not necessarily cause instability. For instance, disruptions such as darkening of the sky appears more continuous than switching off the lights. In change blindness experiments, gradual changes are more difficult to detect, which would lead to perceptual continuity (Simons et al., 2000).

What kinds of exogenous disruptions are perceived as temporally stable and continuous? These questions, when answered, adds precision to our understanding of the exogenous changes that are perceived as continuous.

The most challenging question to answer is perhaps the “why” of perceptual continuity. Why is there a need for perceptual continuity? Why should perception reach temporal stability? Unfortunately, this thesis is unable to address these questions. These questions may perhaps be answered someday by some clever means, or they may continue to remain a mystery. What remains clear is that we do experience the physical world in a continuous manner. Since our experience of the physical world is continuous, perceptual continuity is therefore an important aspect of perception.

Thesis conclusion

Behaviors could maintain perceptual continuity

In this thesis, we enhanced our understanding of temporal stability by investigating the behaviors which could maintain perceptual continuity. Perceptual continuity was the continuous experience of external things involving a conscious completion of missing information which make sense to the observer. Temporal stability arises by comparing the previous and current information. This indicated that serial dependence, a theory with a similar logic, could be associated with temporal stability. In Part 1, we investigated serial dependence and showed that temporal stability was modality-specific because our responses to the visual world appear to be

embedded in perception, and our responses to visual objects become biased by what we previously perceived.

We then argued, in part 2, that temporal stability was not simply a failure of change detection for endogenous disruptions during blinks. Temporal stability also involved other systems to maintain it. The evidence came from our observations that the oculomotor system re-oriented the gaze towards positional changes of an object during the blink. The gaze correction was a feature of the phenomenon: blink adaptation. The oculomotor minimized discrepancies between the object's position during blink adaptation. Thus, the observer remained looking at the object even though the object was in a new position after blinking. Since the oculomotor system behaved in response to positional changes of objects in the external world, this was evidence that temporal stability in vision was achieved by involving the oculomotor to maintain perceptual continuity. We speculated that temporal stability was attainable due to a signal generated during blinking.

The speculation was confirmed in part 3. We showed that saccades to visible objects were more accurate after the observer blinked, as compared to merely fixating before the saccade. This was due to saccade plan updating. We then reasoned that saccade plans were updated to enable a continuous experience of visual exploration because our eyes land where we want them to. Since blinks and saccades are different arms of the oculomotor system, this supported the argument that there was a signal created when blinking. Saccade plans were updated due to this signal which anticipated eye positions after blinking. We also speculated that the oculomotor system could not maintain temporal stability using to this signal alone. Effects from other perspectives of perceptual continuity could also contribute to guide temporal stability

In conclusion, this thesis showed the following behaviors which could maintain perceptual continuity: 1) visual responses are embedded in perception because they are biased by what was previously perceived, as demonstrated through serial dependence, 2) positional changes of a target is minimized across a blink due to blink adaptation, and 3) saccade plans are updated when we blink during visual exploration to visible targets. These three behaviors helped further our understanding of temporal stability, and we arrive at the following definition for temporal stability: Temporal stability, when expressed through serial dependence, is modality-specific. In vision, the oculomotor system maintains temporal stability thanks to a signal produced when blinking. This signal helps to re-orient gaze to positional changes of objects that happen when blinking, or to update saccade plans to ensure that our eyes land accurately onto the target. The oculomotor system cannot ensure temporal stability alone using this signal. Other effects which maintain perceptual continuity also play a role in ensuring temporal stability.

References

- Abdi, H. (2007). Bonferroni Test. In N. J. Salkind (Ed.), *Encyclopedia of measurement and statistics* (pp. 103-107). Thousand Oaks, CA: Sage Publications, Inc.
doi:<http://dx.doi.org/10.4135/9781412952644>
- Adams, W. J., Gray, K. L., Garner, M., & Graf, E. W. (2010). High-level face adaptation without awareness. *Psychological Science*, 21(2), 205-210.
- Agostino, R., Berardelli, A., Cruccu, G., Stocchi, F., & Manfredi, M. (1987). Corneal and blink reflexes in Parkinson's disease with "on - off" fluctuations. *Movement disorders: official journal of the Movement Disorder Society*, 2(4), 227-235.
- Agostino, R., Bologna, M., Dinapoli, L., Gregori, B., Fabbrini, G., Accornero, N., & Berardelli, A. (2008). Voluntary, spontaneous, and reflex blinking in Parkinson's disease. *Movement disorders*, 23(5), 669-675.
- Akaike, H. (Ed.) (1973). *Information theory and an extension of the maximum likelihood principle*. Budapest, Hungary: Akadémiai Kiadó.
- Akande, O. O., & Murphy, P. J. (2005). Estimation of the vocal tract transfer function with application to glottal wave analysis. *Speech Communication*, 46(1), 15-36. doi:<https://doi.org/10.1016/j.specom.2005.01.007>
- Alais, D., Leung, J., & Van der Burg, E. (2017). Linear summation of repulsive and attractive serial dependencies: Orientation and motion dependencies sum in motion perception. *Journal of Neuroscience*, 37(16), 4381-4390.
- Alais, D., Orchard-Mills, E., & Van der Burg, E. (2015). Auditory frequency perception adapts rapidly to the immediate past. *Attention, Perception, & Psychophysics*, 77(3), 896-906.
- Anstis, S. M., MacKay, D. M., Longuet-Higgins, H. C., & Sutherland, N. S. (1980). The perception of apparent movement. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, 290(1038), 153-168.
doi:10.1098/rstb.1980.0088
- Anstis, S. M., Verstraten, F. A., & Mather, G. (1998). The motion aftereffect. *Trends in cognitive sciences*, 2(3), 111-117.
- Arzounian, D., de Kerangal, M., & de Cheveigné, A. (2017). Sequential dependencies in pitch judgments. *The Journal of the Acoustical Society of America*, 142(5), 3047-3057.
- Bahill, A. T., Adler, D., & Stark, L. (1975). Most naturally occurring human saccades have magnitudes of 15 degrees or less. *Investigative Ophthalmology & Visual Science*, 14(6), 468-469.
- Bahill, A. T., Clark, M. R., & Stark, L. (1975a). Dynamic overshoot in saccadic eye movements is caused by neurological control signal reversals. *Experimental neurology*, 48(1), 107-122.
- Bahill, A. T., Clark, M. R., & Stark, L. (1975b). The main sequence, a tool for studying human eye movements. *Mathematical Biosciences*, 24(3-4), 191-204.
- Baloh, R. W., Konrad, H. R., Sills, A. W., & Honrubia, V. (1975). The saccade velocity test. *Neurology*, 25(11), 1071-1071.
- Beale, J. M., & Keil, F. C. (1995). Categorical effects in the perception of faces. *Cognition*, 57(3), 217-239. doi:[https://doi.org/10.1016/0010-0277\(95\)00669-X](https://doi.org/10.1016/0010-0277(95)00669-X)
- Beck, D. M., Rees, G., Frith, C. D., & Lavie, N. (2001). Neural correlates of change detection and change blindness. *Nature neuroscience*, 4(6), 645.
- Becker, W., & Fuchs, A. (1969). Further properties of the human saccadic system: eye movements and correction saccades with and without visual fixation points. *Vision research*, 9(10), 1247-1258.

- Becker, W., & Jürgens, R. (1979). An analysis of the saccadic system by means of double step stimuli. *Vision research*, 19(9), 967-983.
- Bellebaum, C., Hoffmann, K.-P., & Daum, I. (2005). Post-saccadic updating of visual space in the posterior parietal cortex in humans. *Behavioural brain research*, 163(2), 194-203.
- Belmonte, C., & Gallar, J. (2011). Cold thermoreceptors, unexpected players in tear production and ocular dryness sensations. *Investigative Ophthalmology & Visual Science*, 52(6), 3888-3892.
- Bentivoglio, A. R., Bressman, S. B., Cassetta, E., Carretta, D., Tonali, P., & Albanese, A. (1997). Analysis of blink rate patterns in normal subjects. *Movement disorders*, 12(6), 1028-1034.
- Berens, P. (2009). CircStat: A MATLAB Toolbox for Circular Statistics. 2009, 31(10), 21. doi:10.18637/jss.v031.i10
- Biederman, I., & Cooper, E. E. (1992). Size invariance in visual object priming. *Journal of Experimental Psychology: Human Perception and Performance*, 18(1), 121.
- Blake, R., Tadin, D., Sobel, K. V., Raissian, T. A., & Chong, S. C. (2006). Strength of early visual adaptation depends on visual awareness. *Proceedings of the National Academy of Sciences*, 103(12), 4783-4788.
- Bliss, D. P., Sun, J. J., & D'Esposito, M. (2017). Serial dependence is absent at the time of perception but increases in visual working memory. *Scientific reports*, 7(1), 14739.
- Block, N. (2011). Perceptual consciousness overflows cognitive access. *Trends in cognitive sciences*, 15(12), 567-575.
- Bodis-Wollner, I., Bucher, S., & Seelos, K. (1999). Cortical activation patterns during voluntary blinks and voluntary saccades. *Neurology*, 53(8), 1800-1800.
- Boghen, D., Troost, B., Daroff, R., Dell'Osso, L., & Birkett, J. (1974). Velocity characteristics of normal human saccades. *Investigative Ophthalmology & Visual Science*, 13(8), 619-623.
- Bolbecker, A. R., Mehta, C. S., Edwards, C. R., Steinmetz, J. E., O'Donnell, B. F., & Hetrick, W. P. (2009). Eye-blink conditioning deficits indicate temporal processing abnormalities in schizophrenia. *Schizophr Res*, 111(1-3), 182-191. doi:<https://doi.org/10.1016/j.schres.2009.03.016>
- Bonnetblanc, F., & Baraduc, P. (2007). Saccadic adaptation without retinal postsaccadic error. *Neuroreport*, 18(13), 1399-1402.
- Bour, L., Aramideh, M., & De Visser, B. O. (2000). Neurophysiological aspects of eye and eyelid movements during blinking in humans. *Journal of Neurophysiology*, 83(1), 166-176.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial vision*, 10, 433-436.
- Bridgeman, B., & Stark, L. (1991). Ocular proprioception and efference copy in registering visual direction. *Vision research*, 31(11), 1903-1913.
- Bruce, C. J., & Goldberg, M. E. (1985). Primate frontal eye fields. I. Single neurons discharging before saccades. *Journal of Neurophysiology*, 53(3), 603-635.
- Brungart, D. S. (2001). Informational and energetic masking effects in the perception of two simultaneous talkers. *The Journal of the Acoustical Society of America*, 109(3), 1101-1109.
- Buckner, R. L., & Koutstaal, W. (1998). Functional neuroimaging studies of encoding, priming, and explicit memory retrieval. *Proceedings of the National Academy of Sciences*, 95(3), 891-898.

- Bülthoff, I., & Newell, F. (2004). Categorical perception of sex occurs in familiar but not unfamiliar faces. *Visual Cognition*, 11(7), 823-855.
doi:10.1080/13506280444000012
- Burr, D. C., Morrone, M. C., & Ross, J. (1994). Selective suppression of the magnocellular visual pathway during saccadic eye movements. *Nature*, 371(6497), 511.
- Büttner-Ennever, J. A., Horn, A. K., Henn, V., & Cohen, B. (1999). Projections from the superior colliculus motor map to omnipause neurons in monkey. *Journal of Comparative Neurology*, 413(1), 55-67.
- Byrne, D., Lamberth, J., Palmer, J., & London, O. (1969). Sequential effects as a function of explicit and implicit interpolated attraction responses. *Journal of Personality and Social Psychology*, 13(1), 70.
- Campbell, P. E., & Wells, J. F. (1970). Sequential effects of magnitude of delayed reward and magnitude of immediate reward on pattern running and resistance to extinction. *The Psychological Record*, 20(2), 203-210.
- Carandini, M. (2000). Visual cortex: Fatigue and adaptation. *Current Biology*, 10(16), R605-R607.
- Cavanagh, P., Hunt, A. R., Afraz, A., & Rolfs, M. (2010). Visual stability based on remapping of attention pointers. *Trends in cognitive sciences*, 14(4), 147-153.
- Cavanaugh, J., Berman, R. A., Joiner, W. M., & Wurtz, R. H. (2016). Saccadic corollary discharge underlies stable visual perception. *Journal of Neuroscience*, 36(1), 31-42.
- Cave, C. B. (1997). Very long-lasting priming in picture naming. *Psychological Science*, 8(4), 322-325.
- Chen, B., & May, P. J. (2002). Premotor circuits controlling eyelid movements in conjunction with vertical saccades in the cat: I. The rostral interstitial nucleus of the medial longitudinal fasciculus. *Journal of Comparative Neurology*, 450(2), 183-202.
- Chen, B., & May, P. J. (2007). Premotor circuits controlling eyelid movements in conjunction with vertical saccades in the cat: II. Interstitial nucleus of Cajal. *Journal of Comparative Neurology*, 500(4), 676-692.
- Chepesiuk, R. (2005). Decibel Hell: The Effects of Living in a Noisy World. *Environmental Health Perspectives*, 113(1), A34-A41.
doi:doi:10.1289/ehp.113-a34
- Chermahini, S. A., & Hommel, B. (2010). The (b) link between creativity and dopamine: spontaneous eye blink rates predict and dissociate divergent and convergent thinking. *Cognition*, 115(3), 458-465.
- Cicchini, G. M., Anobile, G., & Burr, D. C. (2014). Compressive mapping of number to space reflects dynamic encoding mechanisms, not static logarithmic transform. *Proceedings of the National Academy of Sciences*, 111(21), 7867-7872.
- Cicchini, G. M., Mikellidou, K., & Burr, D. (2017). Serial dependencies act directly on perception. *Journal of vision*, 17(14), 6-6. doi:10.1167/17.14.6
- Clarke, F. (1961). Visual recovery following local adaptation of the peripheral retina (Troxler's effect). *Optica Acta: International Journal of Optics*, 8(2), 121-135.
- Cohen, B., & Feldman, M. (1968). Relationship of electrical activity in pontine reticular formation and lateral geniculate body to rapid eye movements. *Journal of Neurophysiology*, 31(6), 806-817.
- Cohen, J. (1988). Statistical power analysis for the behavioral sciences New York. NY: Academic.

- Cohen, M. A., Horowitz, T. S., & Wolfe, J. M. (2009). Auditory recognition memory is inferior to visual recognition memory. *Proceedings of the National Academy of Sciences*, 106(14), 6008-6010.
- Cohen, R. G., & Rosenbaum, D. A. (2004). Where grasps are made reveals how grasps are planned: generation and recall of motor plans. *Experimental brain research*, 157(4), 486-495.
- Collewijn, H., Erkelens, C. J., & Steinman, R. M. (1988a). Binocular co - ordination of human horizontal saccadic eye movements. *The Journal of physiology*, 404(1), 157-182.
- Collewijn, H., Erkelens, C. J., & Steinman, R. M. (1988b). Binocular co - ordination of human vertical saccadic eye movements. *The Journal of physiology*, 404(1), 183-197.
- Collewijn, H., Erkelens, C. J., & Steinman, R. M. (1995). Voluntary binocular gaze-shifts in the plane of regard: dynamics of version and vergence. *Vision research*, 35(23-24), 3335-3358.
- Collewijn, H., Van Der Steen, J., & Steinman, R. (1985). Human eye movements associated with blinks and prolonged eyelid closure. *Journal of Neurophysiology*, 54(1), 11-27.
- Collins, T., Doré-Mazars, K., & Lappe, M. (2007). Motor space structures perceptual space: Evidence from human saccadic adaptation. *Brain research*, 1172, 32-39.
- Crawford, J., Cadera, W., & Vilis, T. (1991). Generation of torsional and vertical eye position signals by the interstitial nucleus of Cajal. *Science*, 252(5012), 1551-1553.
- Cyr, G. J. S., & Fender, D. H. (1969). The interplay of drifts and flicks in binocular fixation. *Vision research*, 9(2), 245-265.
- Darriba, Á., Pazo-Álvarez, P., Capilla, A., & Amenedo, E. (2012). Oscillatory brain activity in the time frequency domain associated to change blindness and change detection awareness. *Journal of Cognitive Neuroscience*, 24(2), 337-350.
- Dassonville, P., Schlag, J., & Schlag-Rey, M. (1992). The frontal eye field provides the goal of saccadic eye movement. *Experimental brain research*, 89(2), 300-310.
- De Jong, K. (1991). An articulatory study of consonant-induced vowel duration changes in English. *Phonetica*, 48(1), 1-17.
- Deatherage, B. H., & Hirsh, I. J. (1959). Auditory localization of clicks. *The Journal of the Acoustical Society of America*, 31(4), 486-492.
- Deese, J., & Kaufman, R. A. (1957). Serial effects in recall of unorganized and sequentially organized verbal material. *Journal of Experimental Psychology*, 54(3), 180-187. doi:<http://dx.doi.org/10.1037/h0040536>
- Dehaene, S., Naccache, L., Le Clec'H, G., Koechlin, E., Mueller, M., Dehaene-Lambertz, G., . . . Le Bihan, D. (1998). Imaging unconscious semantic priming. *Nature*, 395(6702), 597-600.
- Demonet, J.-F., Chollet, F., Ramsay, S., Cardebat, D., Nespoulous, J.-L., Wise, R., . . . Frackowiak, R. (1992). The anatomy of phonological and semantic processing in normal subjects. *Brain*, 115(6), 1753-1768.
- Deubel, H., Schneider, W. X., & Bridgeman, B. (1996). Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision research*, 36(7), 985-996.

- Deubel, H., Schneider, W. X., & Bridgeman, B. (2002). Transsaccadic memory of position and form. In *Progress in brain research* (Vol. 140, pp. 165-180): Elsevier.
- Deubel, H., Wolf, W., & Hauske, G. (1982). Corrective saccades: Effect of shifting the saccade goal. *Vision research*, 22(3), 353-364.
- Doane, M. G. (1981). Blinking and the Mechanics of the Lacrimal Drainage System. *Ophthalmology*, 88(8), 844-851. doi:[http://dx.doi.org/10.1016/S0161-6420\(81\)34940-9](http://dx.doi.org/10.1016/S0161-6420(81)34940-9)
- Dorris, M. C., & Munoz, D. P. (1998). Saccadic probability influences motor preparation signals and time to saccadic initiation. *Journal of Neuroscience*, 18(17), 7015-7026.
- Dretske, F. (2007). What change blindness teaches about consciousness. *Philosophical Perspectives*, 21, 215-230.
- Driver, J., & Noesselt, T. (2008). Multisensory interplay reveals crossmodal influences on 'sensory-specific' brain regions, neural responses, and judgments. *Neuron*, 57(1), 11-23.
- Driver, P. J., & Lemp, M. A. (1996). Meibomian gland dysfunction. *Survey of ophthalmology*, 40(5), 343-367.
- Efron, B., & Tibshirani, R. (1986). Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. *Statistical science*, 1(1), 54-75.
- Efron, R. (1969). What is Perception? In R. S. Cohen & M. W. Wartofsky (Eds.), *Proceedings of the Boston Colloquium for the Philosophy of Science 1966/1968* (pp. 137-173). Dordrecht: Springer Netherlands.
- Ellis, D. P. W. (2010). Time-domain scrambling of audio signals in Matlab. Retrieved from <http://www.ee.columbia.edu/~dpwe/resources/matlab/scramble/>
- Engbert, R., & Kliegl, R. (2004). Microsaccades keep the eyes' balance during fixation. *Psychological Science*, 15(6), 431-436.
- Enns, J. T., & Di Lollo, V. (1997). Object Substitution: A New Form of Masking in Unattended Visual Locations. *Psychological Science*, 8(2), 135-139. doi:10.1111/j.1467-9280.1997.tb00696.x
- Enns, J. T., Lleras, A., & Moore, C. M. (2010). Object updating: A force for perceptual continuity and scene stability in human vision. *Space and time in perception and action*, 503-520.
- Etcoff, N. L., & Magee, J. J. (1992). Categorical perception of facial expressions. *Cognition*, 44(3), 227-240.
- Eustache, F., Lambert, J., Cassier, C., Dary, M., Rossa, Y., Rioux, P., . . . Lechevalier, B. (1995). Disorders of auditory identification in dementia of the Alzheimer type. *Cortex*, 31(1), 119-127.
- Everling, S., Paré, M., Dorris, M. C., & Munoz, D. P. (1998). Comparison of the discharge characteristics of brain stem omnipause neurons and superior colliculus fixation neurons in monkey: implications for control of fixation and saccade behavior. *Journal of Neurophysiology*, 79(2), 511-528.
- Evinger, C., Kaneko, C., & Fuchs, A. F. (1982). Activity of omnipause neurons in alert cats during saccadic eye movements and visual stimuli. *Journal of Neurophysiology*, 47(5), 827-844.
- Evinger, C., Manning, K. A., Pellegrini, J. J., Basso, M. A., Powers, A. S., & Sibony, P. A. (1994). Not looking while leaping: the linkage of blinking and saccadic gaze shifts. *Experimental brain research*, 100(2), 337-344.

- Evinger, C., Manning, K. A., & Sibony, P. A. (1991). Eyelid movements. Mechanisms and normal data. *Investigative Ophthalmology & Visual Science*, 32(2), 387-400.
- Evinger, C., Shaw, M., Peck, C., Manning, K., & Baker, R. (1984). Blinking and associated eye movements in humans, guinea pigs, and rabbits. *Journal of Neurophysiology*, 52(2), 323-339.
- Fahle, M. (1994). Human pattern recognition: parallel processing and perceptual learning. *Perception*, 23(4), 411-427.
- Favreau, O. E. (1976). Motion aftereffects: evidence for parallel processing in motion perception. *Vision research*, 16(2), 181-186.
- Fechner, G. (1860). *Elemente der Psychophysik*, translated to *Elements of Psychophysics*, translated by HE Adler, 1966. *Holt, Rinehart and Winston, New York*.
- Fender, D., & Julesz, B. (1967). Extension of Panum's fusional area in binocularly stabilized vision. *JOSA*, 57(6), 819-830.
- Ferber, S., Humphrey, G. K., & Vilis, T. (2005). Segregation and persistence of form in the lateral occipital complex. *Neuropsychologia*, 43(1), 41-51. doi:<https://doi.org/10.1016/j.neuropsychologia.2004.06.020>
- Fernandez-Duque, D., & Thornton, I. M. (2000). Change detection without awareness: Do explicit reports underestimate the representation of change in the visual system? *Visual Cognition*, 7(1-3), 323-344.
- Findlay, J. M. (1981). Spatial and temporal factors in the predictive generation of saccadic eye movements. *Vision research*, 21(3), 347-354.
- Fischer, B. (1986). Express saccades in man and monkey. In *Progress in brain research* (Vol. 64, pp. 155-160): Elsevier.
- Fischer, B., & Ramsperger, E. (1984). Human express saccades: extremely short reaction times of goal directed eye movements. *Experimental brain research*, 57(1), 191-195.
- Fischer, B., & Weber, H. (1998). Effects of pre-cues on voluntary and reflexive saccade generation I. Anti-cues for pro-saccades. *Experimental brain research*, 120(4), 403-416.
- Fischer, B., Weber, H., Biscaldi, M., Aiple, F., Otto, P., & Stuhr, V. (1993). Separate populations of visually guided saccades in humans: reaction times and amplitudes. *Experimental brain research*, 92(3), 528-541.
- Fischer, J., & Whitney, D. (2014). Serial dependence in visual perception. *Nat Neurosci*, 17(5), 738-743. doi:10.1038/nn.3689
- Flege, J. E., MacKay, I. R., & Meador, D. (1999). Native Italian speakers' perception and production of English vowels. *The Journal of the Acoustical Society of America*, 106(5), 2973-2987.
- Fogarty, C., & Stern, J. A. (1989). Eye movements and blinks: their relationship to higher cognitive processes. *International Journal of Psychophysiology*, 8(1), 35-42.
- Fornaciai, M., & Park, J. (2018). Attractive serial dependence in the absence of an explicit task. *Psychological Science*, 29(3), 437-446.
- Fornaciai, M., & Park, J. (2019). Serial dependence generalizes across different stimulus formats, but not different sensory modalities. *Vision research*, 160, 108-115. doi:<https://doi.org/10.1016/j.visres.2019.04.011>
- Foxton, J. M., Talcott, J. B., Witton, C., Brace, H., McIntyre, F., & Griffiths, T. D. (2003). Reading skills are related to global, but not local, acoustic pattern perception. *Nature neuroscience*, 6(4), 343.

- Freedman, E. G., & Sparks, D. L. (2000). Coordination of the eyes and head: movement kinematics. *Experimental brain research*, 131(1), 22-32.
- Freeman, J. B., Rule, N. O., Adams, R. B., Jr, & Ambady, N. (2009). The Neural Basis of Categorical Face Perception: Graded Representations of Face Gender in Fusiform and Orbitofrontal Cortices. *Cerebral Cortex*, 20(6), 1314-1322. doi:10.1093/cercor/bhp195
- Fritsche, M., Mostert, P., & de Lange, F. P. (2017). Opposite effects of recent history on perception and decision. *Current Biology*, 27(4), 590-595.
- Fry, D. B., Abramson, A. S., Eimas, P. D., & Liberman, A. M. (1962). The Identification and Discrimination of Synthetic Vowels. *Language and speech*, 5(4), 171-189. doi:10.1177/002383096200500401
- Fuchs, A., Becker, W., Ling, L., Langer, T. P., & Kaneko, C. (1992). Discharge patterns of levator palpebrae superioris motoneurons during vertical lid and eye movements in the monkey. *Journal of Neurophysiology*, 68(1), 233-243.
- Fuchs, A., Kaneko, C., & Scudder, C. (1985). Brainstem control of saccadic eye movements. *Annual review of neuroscience*, 8(1), 307-337.
- Gainotti, G., & Lemmo, M. A. (1976). Comprehension of symbolic gestures in aphasia. *Brain and Language*, 3(3), 451-460.
- Gandhi, N. J., & Bonadonna, D. K. (2005). Temporal interactions of air-puff-evoked blinks and saccadic eye movements: insights into motor preparation. *J Neurophysiol*, 93(3), 1718-1729. doi:10.1152/jn.00854.2004
- Gandhi, N. J., & Keller, E. L. (1997). Spatial distribution and discharge characteristics of superior colliculus neurons antidromically activated from the omnipause region in monkey. *Journal of Neurophysiology*, 78(4), 2221-2225.
- Gandhi, T. K., Singh, A. K., Swami, P., Ganesh, S., & Sinha, P. (2017). Emergence of categorical face perception after extended early-onset blindness. *Proceedings of the National Academy of Sciences*, 114(23), 6139-6143. doi:10.1073/pnas.1616050114
- Gerbino, W., & Salmaso, D. (1987). The effect of amodal completion on visual matching. *Acta psychologica*, 65(1), 25-46.
- Gescheider, G. A. (2013). *Psychophysics: the fundamentals*: Psychology Press.
- Gibson, J. J. (1929). The reproduction of visually perceived forms. *Journal of Experimental Psychology*, 12(1), 1.
- Golan, T., Davidesco, I., Meshulam, M., Groppe, D. M., Mégevand, P., Yeagle, E. M., . . . Schroeder, C. E. (2016). Human intracranial recordings link suppressed transients rather than 'filling-in' to perceptual continuity across blinks. *Elife*, 5, e17243.
- Goldberg, S. J., & Shall, M. S. (1999). Motor units of extraocular muscles: recent findings. In *Progress in brain research* (Vol. 123, pp. 221-232): Elsevier.
- Goossens, H., & Van Opstal, A. (2000a). Blink-Perturbed Saccades in Monkey. I. Behavioral Analysis. *Journal of Neurophysiology*, 83(6), 3411-3429. doi:10.1152/jn.2000.83.6.3411
- Goossens, H., & Van Opstal, A. (2000b). Blink-perturbed saccades in monkey. II. Superior colliculus activity. *Journal of Neurophysiology*, 83(6), 3430-3452.
- Goossens, H., & Van Opstal, A. J. (2006). Dynamic ensemble coding of saccades in the monkey superior colliculus. *Journal of Neurophysiology*, 95(4), 2326-2341.
- Gorea, A., & Lorenceau, J. (1984). Perceptual bistability with counterphase gratings. *Vision research*, 24(10), 1321-1331. doi:[https://doi.org/10.1016/0042-6989\(84\)90187-1](https://doi.org/10.1016/0042-6989(84)90187-1)

- Goto, E., Yagi, Y., Matsumoto, Y., & Tsubota, K. (2002). Impaired functional visual acuity of dry eye patients. *American Journal of Ophthalmology*, 133(2), 181-186.
- Green, D. M., Luce, R. D., & Duncan, J. E. (1977). Variability and sequential effects in magnitude production and estimation of auditory intensity. *Perception & psychophysics*, 22(5), 450-456.
- Griepentrog, G. J., & Lucarelli, M. J. (2011). Functions of the orbit and eyelids. In *Adler's Physiology of the Eye* (pp. 334-335): Elsevier Saunders, Philadelphia.
- Guitton, D., Simard, R., & Codère, F. (1991). Upper eyelid movements measured with a search coil during blinks and vertical saccades. *Investigative Ophthalmology & Visual Science*, 32(13), 3298-3305.
- Hain, T., Zee, D. S., & Mordes, M. (1986). Blink - induced saccadic oscillations. *Annals of Neurology*, 19(3), 299-301.
- Hall, D. A., Johnsrude, I. S., Haggard, M. P., Palmer, A. R., Akeroyd, M. A., & Summerfield, A. Q. (2002). Spectral and temporal processing in human auditory cortex. *Cerebral Cortex*, 12(2), 140-149.
- Haslwanter, T. (2002). Mechanics of eye movements: implications of the "orbital revolution". *Annals of the New York Academy of Sciences*, 956(1), 33-41.
- Havermann, K., & Lappe, M. (2010). The influence of the consistency of postsaccadic visual errors on saccadic adaptation. *Journal of Neurophysiology*, 103(6), 3302-3310.
- Hayhoe, M. M., Shrivastava, A., Mruczek, R., & Pelz, J. B. (2003). Visual memory and motor planning in a natural task. *Journal of vision*, 3(1), 6-6.
- Helson, H. (1964a). Adaptation-level theory.
- Helson, H. (1964b). Current trends and issues in adaptation-level theory. *American psychologist*, 19(1), 26.
- Helson, H., & Nash, M. C. (1960). Anchor, contrast, and paradoxical distance effects. *Journal of Experimental Psychology*, 59(2), 113.
- Hepp, K., & Henn, V. (1983). Spatio-temporal recoding of rapid eye movement signals in the monkey paramedian pontine reticular formation (PPRF). *Experimental brain research*, 52(1), 105-120.
- Hering, E. (1977). *The theory of binocular vision*. Springer, US: Plenum Publishing Corporation.
- Hess, K., Reisine, H., & Dürsteler, M. (1985). Normal eye drift and saccadic drift correction in darkness. *Neuro-ophthalmology*, 5(4), 247-252.
- Higgins, J. S., Irwin, D. E., Wang, R. F., & Thomas, L. E. (2009). Visual direction constancy across eyeblinks. *Attention, Perception, & Psychophysics*, 71(7), 1607-1617.
- Hillenbrand, J., Getty, L. A., Clark, M. J., & Wheeler, K. (1995). Acoustic characteristics of American English vowels. *The Journal of the Acoustical Society of America*, 97(5), 3099-3111.
- Himebaugh, N. L., Begley, C. G., Bradley, A., & Wilkinson, J. A. (2009). Blinking and tear break-up during four visual tasks. *Optometry and Vision Science*, 86(2), E106-E114.
- Hiraoka, M., & Shimamura, M. (1977). Neural mechanisms of the corneal blinking reflex in cats. *Brain research*, 125(2), 265-275.
- Hock, H. S., Kelso, J. S., & Schöner, G. (1993). Bistability and hysteresis in the organization of apparent motion patterns. *Journal of Experimental Psychology: Human Perception and Performance*, 19(1), 63-80. doi:10.1037/0096-1523.19.1.63

- Hock, H. S., Schöner, G., & Giese, M. (2003). The dynamical foundations of motion pattern formation: Stability, selective adaptation, and perceptual continuity. *Perception & psychophysics*, 65(3), 429-457. doi:10.3758/BF03194574
- Hoenig, J. M., & Heisey, D. M. (2001). The abuse of power: the pervasive fallacy of power calculations for data analysis. *The American Statistician*, 55(1), 19-24.
- Hogan, J. T., & Rozsypal, A. J. (1980). Evaluation of vowel duration as a cue for the voicing distinction in the following word - final consonant. *The Journal of the Acoustical Society of America*, 67(5), 1764-1771.
- Holland, M. K., & Lockhead, G. (1968). Sequential effects in absolute judgments of loudness. *Perception & psychophysics*, 3(6), 409-414.
- Holland, M. K., & Tarlow, G. (1972). Blinking and mental load. *Psychological Reports*, 31(1), 119-127.
- Holland, M. K., & Tarlow, G. (1975). Blinking and thinking. *Perceptual and motor skills*, 41(2), 403-406.
- Hollingworth, H. L. (1910). The central tendency of judgment. *The Journal of Philosophy, Psychology and Scientific Methods*, 7(17), 461-469.
- Horn, A. K., Büttner-Ennever, J. A., & Büttner, U. (1996). Saccadic premotor neurons in the brainstem: functional neuroanatomy and clinical implications. *Neuro-ophthalmology*, 16(4), 229-240.
- Huang, L., Holcombe, A. O., & Pashler, H. (2004). Repetition priming in visual search: Episodic retrieval, not feature priming. *Memory & Cognition*, 32(1), 12-20.
- Huetzel, S. A., Güzelde, G., & McCarthy, G. (2001). Dissociating the neural mechanisms of visual attention in change detection using functional MRI. *Journal of Cognitive Neuroscience*, 13(7), 1006-1018.
- Humphreys, G. W., Duncan, J., Treisman, A., & Treisman, A. (1998). Feature binding, attention and object perception. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 353(1373), 1295-1306. doi:doi:10.1098/rstb.1998.0284
- IBM-Corp. (2011). IBM SPSS Statistics for Windows, Version 20.0. Armonk, NY: IBM Corp.
- Irwin, D. E. (1992). Memory for position and identity across eye movements. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 18(2), 307.
- Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J. L., & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences*, 96(16), 9379-9384. doi:10.1073/pnas.96.16.9379
- Jesteadt, W., Luce, R. D., & Green, D. M. (1977). Sequential effects in judgments of loudness. *Journal of Experimental Psychology: Human Perception and Performance*, 3(1), 92-104. doi:<http://dx.doi.org/10.1037/0096-1523.3.1.92>
- Jones, R. R., Weinrott, M. R., & Vaught, R. S. (1978). Effects of serial dependency on the agreement between visual and statistical inference. *Journal of Applied Behavior Analysis*, 11(2), 277-283.
- Jonikaitis, D., Szinte, M., Rolf, M., & Cavanagh, P. (2012). Allocation of attention across saccades. *American Journal of Physiology-Heart and Circulatory Physiology*.
- Kahneman, D. (1968). Method, findings, and theory in studies of visual masking. *Psychological Bulletin*, 70(6p1), 404.

- Kalesnykas, R., & Hallett, P. (1987). The differentiation of visually guided and anticipatory saccades in gap and overlap paradigms. *Experimental brain research*, 68(1), 115-121.
- Kaneko, K., & Sakamoto, K. (1999). Evaluation of three types of blinks with the use of electro-oculogram and electromyogram. *Perceptual and motor skills*, 88(3), 1037-1052.
- Kanizsa, G. (1979). Organization in vision: Essays on Gestalt psychology. *Nova Iorque: Praeger*.
- Kanizsa, G. (1985). Seeing and thinking. *Acta psychologica*, 59(1), 23-33.
- Kapoula, Z., Robinson, D. A., & Hain, T. (1986). Motion of the eye immediately after a saccade. *Experimental brain research*, 61(2), 386-394.
- Karson, C. N. (1983). Spontaneous eye-blink rates and dopaminergic systems. *Brain*, 106(3), 643-653.
- Karson, C. N., Berman, K. F., Donnelly, E. F., Mendelson, W. B., Kleinman, J. E., & Wyatt, R. J. (1981). Speaking, thinking, and blinking. *Psychiatry research*, 5(3), 243-246.
- Keck, M. J., & Pentz, B. (1977). Recovery from adaptation to moving gratings. *Perception*, 6(6), 719-725.
- Kentridge, R. W., Nijboer, T. C., & Heywood, C. A. (2008). Attended but unseen: Visual attention is not sufficient for visual awareness. *Neuropsychologia*, 46(3), 864-869.
- Khazali, M. F., Pomper, J. K., Smilgin, A., Bunjes, F., & Thier, P. (2016). A new motor synergy that serves the needs of oculomotor and eye lid systems while keeping the downtime of vision minimal. *Elife*, 5. doi:10.7554/eLife.16290
- Khazali, M. F., Pomper, J. K., & Thier, P. (2017). Blink associated resetting eye movements (BARMs) are functionally complementary to microsaccades in correcting for fixation errors. *Scientific reports*, 7(1), 16823.
- Kimura, J., Powers, J. M., & Van Allen, M. W. (1969). Reflex response of orbicularis oculi muscle to supraorbital nerve stimulation: Study in normal subjects and in peripheral facial paresis. *Archives of neurology*, 21(2), 193-199.
- Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007). What's new in Psychtoolbox-3. *Perception*, 36(14), 1-16.
- Koelsch, S., Kasper, E., Sammler, D., Schulze, K., Gunter, T., & Friederici, A. D. (2004). Music, language and meaning: brain signatures of semantic processing. *Nature neuroscience*, 7(3), 302.
- Koivisto, M., & Revonsuo, A. (2003). An ERP study of change detection, change blindness, and visual awareness. *Psychophysiology*, 40(3), 423-429.
- Korošec, M., Zidar, I., Reits, D., Evinger, C., & Vanderwerf, F. (2006). Eyelid movements during blinking in patients with Parkinson's disease. *Movement disorders*, 21(8), 1248-1251.
- Kosovicheva, A. A., Wolfe, B. A., & Whitney, D. (2014). Visual motion shifts saccade targets. *Attention, Perception, & Psychophysics*, 76(6), 1778-1788.
- Kuhl, P. K. (1991). Human adults and human infants show a "perceptual magnet effect" for the prototypes of speech categories, monkeys do not. *Perception & psychophysics*, 50(2), 93-107.
- Kuhn, G., & Tatler, B. W. (2005). Magic and fixation: Now you don't see it, now you do. *Perception*, 34(9), 1155-1161.
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2015). Package 'lmerTest'. *R package version*, 2(0).

- Lages, M., & Treisman, M. (1998). Spatial frequency discrimination: visual long-term memory or criterion setting? *Vision research*, 38(4), 557-572.
- Lamme, V. A. (2003). Why visual attention and awareness are different. *Trends in cognitive sciences*, 7(1), 12-18.
- Large, M.-E., Aldcroft, A., & Vilis, T. (2005). Perceptual Continuity and the Emergence of Perceptual Persistence in the Ventral Visual Pathway. *Journal of Neurophysiology*, 93(6), 3453-3462. doi:10.1152/jn.00934.2004
- Lau, W. K., & Maus, G. W. (2019a). Directional biases for blink adaptation in voluntary and reflexive eye blinks. *Journal of vision*, 19(3), 13-13.
- Lau, W. K., & Maus, G. W. (2019b). Visual serial dependence in an audiovisual stimulus. *Journal of vision*, 19(13), 20-20.
- Lawrence, M. S., & Redmond, D. E. (1991). MPTP lesions and dopaminergic drugs alter eye blink rate in African green monkeys. *Pharmacology Biochemistry and Behavior*, 38(4), 869-874. doi:[https://doi.org/10.1016/0091-3057\(91\)90255-Z](https://doi.org/10.1016/0091-3057(91)90255-Z)
- Lawson, R. W. (1948a). Blinking, its role in physical measurements. *Nature*, 161(4083), 154-157.
- Lawson, R. W. (1948b). Photographic evaluation of blackout indices. *Nature*, 162, 531-532.
- Lazar, N. (2011). Bayes Factors. In N. J. Salkind (Ed.), *Encyclopedia of Measurements and Statistics* (pp. 75-76). Thousand Oaks, CA: Sage Publications, Inc. doi:<https://dx.doi.org/10.4135/9781412952644>
- Lee, C., Rohrer, W. H., & Sparks, D. L. (1988). Population coding of saccadic eye movements by neurons in the superior colliculus. *Nature*, 332(6162), 357.
- Lewald, J., & Ehrenstein, W. H. (1996). The effect of eye position on auditory lateralization. *Experimental brain research*, 108(3), 473-485.
- Liberman, A., Fischer, J., & Whitney, D. (2014). Serial dependence in the perception of faces. *Curr Biol*, 24(21), 2569-2574. doi:10.1016/j.cub.2014.09.025
- Liberman, A., Manassi, M., & Whitney, D. (2018). Serial dependence promotes the stability of perceived emotional expression depending on face similarity. *Attention, Perception, & Psychophysics*, 80(6), 1461-1473. doi:<https://doi.org/10.3758/s13414-018-1533-8>
- Liberman, A. M., Harris, K. S., Hoffman, H. S., & Griffith, B. C. (1957). The discrimination of speech sounds within and across phoneme boundaries. *Journal of Experimental Psychology*, 54(5), 358.
- Logan, G. D. (1990). Repetition priming and automaticity: Common underlying mechanisms? *Cognitive Psychology*, 22(1), 1-35.
- Lord, M. P., & Wright, W. (1948). Eye movements during monocular fixation. *Nature*, 162, 25-26.
- Lu, X., Matsuzawa, M., & Hikosaka, O. (2002). A neural correlate of oculomotor sequences in supplementary eye field. *Neuron*, 34(2), 317-325.
- Makowski, D., Ben-Shachar, M. S., & Lüdecke, D. (2019). bayestestR: Describing effects and their uncertainty, existence and significance within the Bayesian framework. *Journal of Open Source Software*, 4(40), 1541.
- Manassi, M., Liberman, A., Kosovicheva, A., Zhang, K., & Whitney, D. (2018). Serial dependence in position occurs at the time of perception. *Psychonomic Bulletin & Review*, 25(6), 2245-2253.
- Manning, K. A., Riggs, L. A., & Komenda, J. K. (1983). Reflex eyeblinks and visual suppression. *Attention, Perception, & Psychophysics*, 34(3), 250-256.

- Martens, U., Leuthold, H., & Schweinberger, S. R. (2010). Parallel processing in face perception. *Journal of Experimental Psychology: Human Perception and Performance*, 36(1), 103.
- Martinez-Conde, S., Macknik, S. L., Troncoso, X. G., & Dyar, T. A. (2006). Microsaccades counteract visual fading during fixation. *Neuron*, 49(2), 297-305.
- Martinez-Conde, S., Otero-Millan, J., & Macknik, S. L. (2013). The impact of microsaccades on vision: towards a unified theory of saccadic function. *Nature Reviews Neuroscience*, 14(2), 83.
- Mathworks Inc., N. M., USA. (2015). MATLAB R2015a. Natick, Massachusetts, United States: The MathWorks, Inc.
- Maus, G. W., Duyck, M., Lisi, M., Collins, T., Whitney, D., & Cavanagh, P. (2017). Target displacements during eye blinks trigger automatic recalibration of gaze direction. *Current Biology*, 27(3), 445-450.
- Mays, L. E., & Morrissey, D. W. (1995). Electrical stimulation of the pontine omnipause area inhibits eye blink. *Journal of the American Optometric Association*, 66(7), 419-422.
- Mazza, V., Turatto, M., & Umiltà, C. (2005). Foreground-background segmentation and attention: A change blindness study. *Psychological research*, 69(3), 201-210.
- McFadden, D., & Pasanen, E. G. (1976). Lateralization at high frequencies based on interaural time differences. *The Journal of the Acoustical Society of America*, 59(3), 634-639.
- McFarland, J. L., & Fuchs, A. F. (1992). Discharge patterns in nucleus prepositus hypoglossi and adjacent medial vestibular nucleus during horizontal eye movement in behaving macaques. *Journal of Neurophysiology*, 68(1), 319-332.
- Medendorp, W. P., Goltz, H. C., & Vilis, T. (2005). Remapping the remembered target location for anti-saccades in human posterior parietal cortex. *Journal of Neurophysiology*, 94(1), 734-740.
- Medendorp, W. P., Goltz, H. C., Vilis, T., & Crawford, J. D. (2003). Gaze-centered updating of visual space in human parietal cortex. *Journal of Neuroscience*, 23(15), 6209-6214.
- Mehrgardt, S., & Mellert, V. (1977). Transformation characteristics of the external human ear. *The Journal of the Acoustical Society of America*, 61(6), 1567-1576.
- Melcher, D., & Morrone, C. (2007). Transsaccadic memory: Building a stable world from glance to glance. In *Eye Movements* (pp. 213-233): Elsevier.
- Metz, H. S. (1980). Saccades with limited downward gaze. *Archives of Ophthalmology*, 98(12), 2204-2205.
- Middlebrooks, J. C., & Green, D. M. (1991). Sound localization by human listeners. *Annual review of psychology*, 42(1), 135-159.
- Miller, J. M., & Robins, D. (1992). Extraocular muscle forces in alert monkey. *Vision research*, 32(6), 1099-1113.
- Mirpour, K., & Bisley, J. W. (2015). Remapping, spatial stability, and temporal continuity: from the pre-saccadic to postsaccadic representation of visual space in LIP. *Cerebral Cortex*, 26(7), 3183-3195.
- Missal, M., De Brouwer, S., Lefèvre, P., & Olivier, E. (2000). Activity of mesencephalic vertical burst neurons during saccades and smooth pursuit. *Journal of Neurophysiology*, 83(4), 2080-2092.

- Miyawaki, K., Jenkins, J. J., Strange, W., Liberman, A. M., Verbrugge, R., & Fujimura, O. (1975). An effect of linguistic experience: The discrimination of [r] and [l] by native speakers of Japanese and English. *Perception & psychophysics*, 18(5), 331-340.
- Moore, C. M., & Egeth, H. (1997). Perception without attention: Evidence of grouping under conditions of inattention. *Journal of Experimental Psychology: Human Perception and Performance*, 23(2), 339.
- Munoz, D. P. (2002). Commentary: saccadic eye movements: overview of neural circuitry. In *Progress in brain research* (Vol. 140, pp. 89-96): Elsevier.
- Munoz, D. P., Waitzman, D. M., & Wurtz, R. H. (1996). Activity of neurons in monkey superior colliculus during interrupted saccades. *Journal of Neurophysiology*, 75(6), 2562-2580.
- Munoz, D. P., & Wurtz, R. H. (1995). Saccade-related activity in monkey superior colliculus. I. Characteristics of burst and buildup cells. *Journal of Neurophysiology*, 73(6), 2313-2333.
- Murdock Jr, B. B. (1962). The serial position effect of free recall. *Journal of Experimental Psychology*, 64(5), 482.
- Nakamori, K., Odawara, M., Nakajima, T., Mizutani, T., & Tsubota, K. (1997). Blinking is controlled primarily by ocular surface conditions. *American Journal of Ophthalmology*, 124(1), 24-30.
- Nassi, J. J., & Callaway, E. M. (2009). Parallel processing strategies of the primate visual system. *Nature Reviews Neuroscience*, 10(5), 360-372.
- Niedeggen, M., Wichmann, P., & Stoerig, P. (2001). Change blindness and time to consciousness. *European Journal of Neuroscience*, 14(10), 1719-1726.
- Noë, A. (2005). What does change blindness teach us about consciousness? *Trends in cognitive sciences*, 9(5), 218.
- Noë, A., Pessoa, L., & Thompson, E. (2000). Beyond the grand illusion: What change blindness really teaches us about vision. *Visual Cognition*, 7(1-3), 93-106.
- Noto, C. T., & Robinson, F. R. (2001). Visual error is the stimulus for saccade gain adaptation. *Cognitive Brain Research*, 12(2), 301-305.
- O'Keefe, D. J. (2007). Brief report: post hoc power, observed power, a priori power, retrospective power, prospective power, achieved power: sorting out appropriate uses of statistical power analyses. *Communication methods and measures*, 1(4), 291-299.
- O'Regan, J. K., Deubel, H., Clark, J. J., & Rensink, R. A. (2000). Picture changes during blinks: Looking without seeing and seeing without looking. *Visual Cognition*, 7(1-3), 191-211.
- O'Regan, J. K., & Noë, A. (2001). A sensorimotor account of vision and visual consciousness. *Behavioral and Brain Sciences*, 24(5), 939-973.
- Oden, G. C., & Massaro, D. W. (1978). Integration of featural information in speech perception. *Psychological review*, 85(3), 172.
- Ohl, S., Brandt, S. A., & Kliegl, R. (2013). The generation of secondary saccades without postsaccadic visual feedback. *Journal of vision*, 13(5), 11-11.
- Ohtsuka, K., Sawa, M., & Takeda, M. (1989). Accuracy of memory-guided saccades. *Ophthalmologica*, 198(1), 53-56.
- Omori, K., Kojima, H., Kakani, R., Slavits, D. H., & Blaugrund, S. M. (1997). Acoustic characteristics of rough voice: subharmonics. *Journal of Voice*, 11(1), 40-47.
- Oppenheim, A. V. (1999). *Discrete-time signal processing*: Pearson Education India.
- Optican, L. M., & Robinson, D. A. (1980). Cerebellar-dependent adaptive control of primate saccadic system. *Journal of Neurophysiology*, 44(6), 1058-1076.

- Orchard, L. N., & Stern, J. A. (1991). Blinks as an index of cognitive activity during reading. *Integrative Physiological and Behavioral Science*, 26(2), 108-116.
- Paeye, C., Collins, T., & Cavanagh, P. (2017). Transsaccadic perceptual fusion. *Journal of vision*, 17(1), 14-14.
- Pascucci, D., Mancuso, G., Santandrea, E., Della Libera, C., Plomp, G., & Chelazzi, L. (2019). Laws of concatenated perception: Vision goes for novelty, decisions for perseverance. *PLoS biology*, 17(3), e3000144.
- Peli, E., & McCormack, G. (1986). Blink vergence in an antimetropic patient. *Am J Optom Physiol Opt*, 63, 981-984.
- Peterson, G. E., & Barney, H. L. (1952). Control methods used in a study of the vowels. *The Journal of the Acoustical Society of America*, 24(2), 175-184.
- Plenge, G. (1974). On the differences between localization and lateralization. *The Journal of the Acoustical Society of America*, 56(3), 944-951.
- Poletti, M., & Rucci, M. (2016). A compact field guide to the study of microsaccades: Challenges and functions. *Vision research*, 118, 83-97.
- Ponder, E., & Kennedy, W. (1927). On the act of blinking. *Quarterly Journal of Experimental Physiology*, 18(2), 89-110.
- Prablanc, C., & Jeannerod, M. (1975). Corrective saccades: dependence on retinal reafferent signals. *Vision research*, 15(4), 465-469.
- Prime, S. L., Niemeier, M., & Crawford, J. (2006). Transsaccadic integration of visual features in a line intersection task. *Experimental brain research*, 169(4), 532-548.
- Prime, S. L., Tsotsos, L., Keith, G. P., & Crawford, J. D. (2007). Visual memory capacity in transsaccadic integration. *Experimental brain research*, 180(4), 609-628.
- Ptito, M., Schneider, F. C., Paulson, O. B., & Kupers, R. (2008). Alterations of the visual pathways in congenital blindness. *Experimental brain research*, 187(1), 41-49.
- Ramachandran, V., & Anstis, S. M. (1985). Perceptual Organization in Multistable Apparent Motion. *Perception*, 14(2), 135-143. doi:10.1068/p140135
- Rambold, H., Sprenger, A., & Helmchen, C. (2002). Effects of Voluntary Blinks on Saccades, Vergence Eye Movements, and Saccade-Vergence Interactions in Humans. *Journal of Neurophysiology*, 88(3), 1220-1233. doi:10.1152/jn.2002.88.3.1220
- Ramsey, J. L., Langlois, J. H., Hoss, R. A., Rubenstein, A. J., & Griffin, A. M. (2004). Origins of a stereotype: categorization of facial attractiveness by 6-month-old infants. *Developmental Science*, 7(2), 201-211. doi:10.1111/j.1467-7687.2004.00339.x
- Rauschecker, J. P., & Scott, S. K. (2009). Maps and streams in the auditory cortex: nonhuman primates illuminate human speech processing. *Nature neuroscience*, 12(6), 718.
- Ray, S., Schall, J. D., & Murthy, A. (2004). Programming of double-step saccade sequences: modulation by cognitive control. *Vision research*, 44(23), 2707-2718.
- Repp, B. H. (1977). Dichotic competition of speech sounds: The role of acoustic stimulus structure. *Journal of Experimental Psychology: Human Perception and Performance*, 3(1), 37.
- Richards, W. (1969). Saccadic Suppression*. *JOSA*, 59(5), 617-623.

- Ridder, W. H., 3rd, & Tomlinson, A. (1995). Spectral characteristics of blink suppression in normal observers. *Vision Res*, 35(18), 2569-2578. doi:[https://doi.org/10.1016/0042-6989\(95\)00011-N](https://doi.org/10.1016/0042-6989(95)00011-N)
- Riggs, L. A., Kelly, J. P., Manning, K. A., & Moore, R. K. (1987). Blink-related eye movements. *Investigative Ophthalmology & Visual Science*, 28(2), 334-342.
- Riggs, L. A., Volkmann, F. C., & Moore, R. K. (1981). Suppression of the blackout due to blinks. *Vision research*, 21(7), 1075-1079.
- Robinson, D. A. (1972). Eye movements evoked by collicular stimulation in the alert monkey. *Vision research*, 12(11), 1795-1808.
- Robinson, D. A. (1981). Control of eye movements. *Handbook of physiology*, 2(Part 2), 1275-1320.
- Rolf, M. (2009). Microsaccades: Small steps on a long way. *Vision research*, 49(20), 2415-2441. doi:<https://doi.org/10.1016/j.visres.2009.08.010>
- Rolf, M. (2015). Attention in active vision: A perspective on perceptual continuity across saccades. *Perception*, 44(8-9), 900-919.
- Rolf, M., Jonikaitis, D., Deubel, H., & Cavanagh, P. (2011). Predictive remapping of attention across eye movements. *Nature neuroscience*, 14(2), 252.
- Rolf, M., Knapen, T., & Cavanagh, P. (2010). Global saccadic adaptation. *Vision research*, 50(18), 1882-1890. doi:<https://doi.org/10.1016/j.visres.2010.06.010>
- Roseboom, W. (2019). Serial dependence in timing perception. *Journal of Experimental Psychology: Human Perception and Performance*, 45(1), 100-110. doi:<http://dx.doi.org/10.1037/xhp0000591>
- Rottach, K. G., Das, V. E., Wohlgenuth, W., Zivotofsky, A. Z., & Leigh, R. J. (1998). Properties of Horizontal Saccades Accompanied by Blinks. *Journal of Neurophysiology*, 79(6), 2895-2902. doi:10.1152/jn.1998.79.6.2895
- Rushworth, M. F. (2008). Intention, choice, and the medial frontal cortex. *Annals of the New York Academy of Sciences*, 1124(1), 181-207.
- Sams, M., Hari, R., Rif, J., & Knuutila, J. (1993). The human auditory sensory memory trace persists about 10 sec: neuromagnetic evidence. *Journal of Cognitive Neuroscience*, 5(3), 363-370.
- Sayers, B. M. (1964). Acoustic - Image Lateralization Judgments with Binaural Tones. *The Journal of the Acoustical Society of America*, 36(5), 923-926.
- Schacter, D. L. (1992). Priming and multiple memory systems: Perceptual mechanisms of implicit memory. *Journal of Cognitive Neuroscience*, 4(3), 244-256.
- Schacter, D. L., & Badgaiyan, R. D. (2001). Neuroimaging of priming: New perspectives on implicit and explicit memory. *Current directions in psychological science*, 10(1), 1-4.
- Schönbrodt, F. D., & Wagenmakers, E.-J. (2018). Bayes factor design analysis: Planning for compelling evidence. *Psychonomic Bulletin & Review*, 25(1), 128-142.
- Schultz, K. P., Williams, C. R., & Busetini, C. (2010). Macaque pontine omnipause neurons play no direct role in the generation of eye blinks. *Journal of Neurophysiology*, 103(4), 2255-2274.
- Schwartz, J.-L., Abry, C., Boë, L.-J., Ménard, L., & Vallée, N. (2005). Asymmetries in vowel perception, in the context of the Dispersion-Focalisation Theory. *Speech Communication*, 45(4), 425-434.
- Scudder, C. A., Fuchs, A. F., & Langer, T. P. (1988). Characteristics and functional identification of saccadic inhibitory burst neurons in the alert monkey. *Journal of Neurophysiology*, 59(5), 1430-1454.

- Scudder, C. A., Kaneko, C. R., & Fuchs, A. F. (2002). The brainstem burst generator for saccadic eye movements. *Experimental brain research*, 142(4), 439-462.
- Seidler, R. D., Bo, J., & Anguera, J. A. (2012). Neurocognitive contributions to motor skill learning: the role of working memory. *Journal of Motor Behavior*, 44(6), 445-453.
- Shahani, B. (1970). The human blink reflex. *Journal of Neurology, Neurosurgery & Psychiatry*, 33(6), 792-800.
- Shaikh, A. G., Wong, A. L., Optican, L. M., Miura, K., Solomon, D., & Zee, D. S. (2010). Sustained eye closure slows saccades. *Vision research*, 50(17), 1665-1675.
- Shen, K., & Paré, M. (2007). Neuronal activity in superior colliculus signals both stimulus identity and saccade goals during visual conjunction search. *Journal of vision*, 7(5), 15-15.
- Shibutani, H., Sakata, H., & Hyvärinen, J. (1984). Saccade and blinking evoked by microstimulation of the posterior parietal association cortex of the monkey. *Experimental brain research*, 55(1), 1-8.
- Shima, K., Mushiake, H., Saito, N., & Tanji, J. (1996). Role for cells in the presupplementary motor area in updating motor plans. *Proceedings of the National Academy of Sciences*, 93(16), 8694-8698.
- Shimamura, A. P. (1986). Priming effects in amnesia: Evidence for a dissociable memory function. *The Quarterly Journal of Experimental Psychology*, 38(4), 619-644.
- Silverstein, L. D., Graham, F. K., & Bohlin, G. (1981). Selective Attention Effects on the Reflex Blink. *Psychophysiology*, 18(3), 240-247. doi:10.1111/j.1469-8986.1981.tb03026.x
- Simons, D. J., Chabris, C. F., Schnur, T., & Levin, D. T. (2002). Evidence for preserved representations in change blindness. *Consciousness and Cognition*, 11(1), 78-97.
- Simons, D. J., Franconeri, S. L., & Reimer, R. L. (2000). Change blindness in the absence of a visual disruption. *Perception*, 29(10), 1143-1154.
- Simons, D. J., & Levin, D. T. (1997). Change blindness. *Trends in cognitive sciences*, 1(7), 261-267.
- Skavenski, A. A., & Steinman, R. M. (1970). Control of eye position in the dark. *Vision research*, 10(2), 193-203.
- Slater-Hammel, A. T. (1953). Blackout interval during eye blinks. *Research Quarterly. American Association for Health, Physical Education and Recreation*, 24(3), 362-367.
- Smith, A., May, J., & Lyman, R. (1983). Pitch shifts contingent on the modulation frequency of an adaptation tone. *The Journal of the Acoustical Society of America*, 73(2), 691-693.
- Smith, S. (2011). MATLAB Audio Toolkit: University of Massachusetts Lowell. Retrieved from <http://www.cs.uml.edu/~stu/>
- Smith, T., Lamont, P., & Henderson, J. (2012). The penny drops: Change blindness at fixation. *Perception*, 41(4), 489-492.
- Sparks, D. L. (1978). Functional properties of neurons in the monkey superior colliculus: coupling of neuronal activity and saccade onset. *Brain research*, 156(1), 1-16.
- Sparks, D. L., & Mays, L. E. (1990). Signal transformations required for the generation of saccadic eye movements. *Annual review of neuroscience*, 13(1), 309-336.

- Sperry, R. W. (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. *Journal of comparative and physiological psychology*, 43(6), 482.
- Srimal, R., & Curtis, C. E. (2010). Secondary adaptation of memory-guided saccades. *Experimental brain research*, 206(1), 35-46.
- Stahl, J. S. (1999). Amplitude of human head movements associated with horizontal saccades. *Experimental brain research*, 126(1), 41-54.
- Stefan, A. M., Gronau, Q. F., Schönbrodt, F. D., & Wagenmakers, E.-J. (2019). A tutorial on Bayes Factor Design Analysis using an informed prior. *Behavior research methods*, 51(3), 1042-1058.
- Stein, T., & Sterzer, P. (2011). High-level face shape adaptation depends on visual awareness: evidence from continuous flash suppression. *Journal of vision*, 11(8), 5-5.
- Stern, J. A., Walrath, L. C., & Goldstein, R. (1984). The Endogenous Eyeblink. *Psychophysiology*, 21(1), 22-33. doi:10.1111/j.1469-8986.1984.tb02312.x
- Stevens, S. S. (1961). To honor Fechner and repeal his law. *Science*, 133(3446), 80-86.
- Stevens, S. S. (1966). Matching functions between loudness and ten other continua. *Attention, Perception, & Psychophysics*, 1(1), 5-8.
- Strassman, A., Highstein, S., & McCrea, R. (1986). Anatomy and physiology of saccadic burst neurons in the alert squirrel monkey. II. Inhibitory burst neurons. *Journal of Comparative Neurology*, 249(3), 358-380.
- Summerfield, C., & Egner, T. (2009). Expectation (and attention) in visual cognition. *Trends in cognitive sciences*, 13(9), 403-409.
- Tamietto, M., & Morrone, M. C. (2016). Visual plasticity: blindsight bridges anatomy and function in the visual system. *Current Biology*, 26(2), R70-R73.
- Taubert, J., Alais, D., & Burr, D. (2016). Different coding strategies for the perception of stable and changeable facial attributes. *Scientific reports*, 6, 32239.
- Taubert, J., Van der Burg, E., & Alais, D. (2016). Love at second sight: Sequential dependence of facial attractiveness in an on-line dating paradigm. *Scientific reports*, 6, 22740.
- Team, R. (2020). RStudio: Integrated Development for R. Boston, MA: RStudio, PBC. Retrieved from <http://www.rstudio.com/>
- Tian, J., Ying, H. S., & Zee, D. S. (2013). Revisiting corrective saccades: Role of visual feedback. *Vision research*, 89, 54-64.
- Tillmann, B., Schulze, K., & Foxton, J. M. (2009). Congenital amusia: A short-term memory deficit for non-verbal, but not verbal sounds. *Brain and cognition*, 71(3), 259-264.
- Tinelli, F., Cicchini, G. M., Arrighi, R., Tosetti, M., Cioni, G., & Morrone, M. C. (2013). Blindsight in children with congenital and acquired cerebral lesions. *Cortex*, 49(6), 1636-1647.
- Toda, I., Fujishima, H., & Tsubota, K. (1993). Ocular fatigue is the major symptom of dry eye. *Acta ophthalmologica*, 71(3), 347-352.
- Treisman, M., & Williams, T. C. (1984). A theory of criterion setting with an application to sequential dependencies. *Psychological review*, 91(1), 68-111. doi:<http://dx.doi.org/10.1037/0033-295X.91.1.68>
- Tse, P. U. (2004). Mapping visual attention with change blindness: New directions for a new method. *Cognitive science*, 28(2), 241-258.
- Tsubota, K. (1998). Tear dynamics and dry eye. *Progress in retinal and eye research*, 17(4), 565-596.

- Tsubota, K., & Nakamori, K. (1993). Dry eyes and video display terminals. *New England Journal of Medicine*, 328(8), 584-584.
- Tulving, E., & Schacter, D. L. (1990). Priming and human memory systems. *Science*, 247(4940), 301-306.
- Turner, W. D. (1931). Intra-serial effects with lifted weights. *The American Journal of Psychology*, 43(1), 1-25.
- Twaddell, W. F. (1935). On defining the phoneme. *Language*, 11(1), 5-62.
- Ueda, Y., Tominaga, A., Kajimura, S., & Nomura, M. (2016). Spontaneous eye blinks during creative task correlate with divergent processing. *Psychological research*, 80(4), 652-659.
- Valls-Sole, J. (2012). Assessment of excitability in brainstem circuits mediating the blink reflex and the startle reaction. *Clinical Neurophysiology*, 123(1), 13-20.
- Van Ooijen, B. (1996). Vowel mutability and lexical selection in English: Evidence from a word reconstruction task. *Memory & Cognition*, 24(5), 573-583.
- Venables, W. N., & Ripley, B. D. (2013). *Modern applied statistics with S-PLUS*: Springer Science & Business Media.
- Vergilino-Perez, D., & Beauvillain, C. (2004). The ability of the saccadic system to change motor plans in scanning letter strings. *Psychonomic Bulletin & Review*, 11(2), 332-337.
- Vergilino, D., & Beauvillain, C. (2000). The planning of refixation saccades in reading. *Vision research*, 40(25), 3527-3538.
- Vergilino, D., & Beauvillain, C. (2001). Reference frames in reading: evidence from visually and memory-guided saccades. *Vision research*, 41(25-26), 3547-3557.
- Vilis, T., Hepp, K., Schwarz, U., & Henn, V. (1989). On the generation of vertical and torsional rapid eye movements in the monkey. *Experimental brain research*, 77(1), 1-11.
- Volkman, F. C. (1986). Human visual suppression. *Vision research*, 26(9), 1401-1416.
- Volkman, F. C., Riggs, L. A., Ellicott, A. G., & Moore, R. K. (1982). Measurements of visual suppression during opening, closing and blinking of the eyes. *Vision research*, 22(8), 991-996.
- Volkman, F. C., Riggs, L. A., & Moore, R. K. (1980). Eyeblinks and visual suppression. *Science*, 207(4433), 900-902.
- von Noorden, G. K. (1970). Congenital hereditary ptosis with inferior rectus fibrosis: Report of two cases. *Archives of Ophthalmology*, 83(3), 378-380.
- Wallman, J., & Fuchs, A. F. (1998). Saccadic gain modification: visual error drives motor adaptation. *Journal of Neurophysiology*, 80(5), 2405-2416.
- Warrier, C., Wong, P., Penhune, V., Zatorre, R., Parrish, T., Abrams, D., & Kraus, N. (2009). Relating structure to function: Heschl's gyrus and acoustic processing. *Journal of Neuroscience*, 29(1), 61-69.
- Weber, H., Dürr, N., & Fischer, B. (1998). Effects of pre-cues on voluntary and reflexive saccade generation II. Pro-cues for anti-saccades. *Experimental brain research*, 120(4), 417-431.
- Westheimer, G. (1954). Mechanism of saccadic eye movements. *AMA Archives of Ophthalmology*, 52(5), 710-724.
- Wickham, H. (2016). *ggplot2: elegant graphics for data analysis*: Springer.
- Wightman, F. L., & Kistler, D. J. (1989). Headphone simulation of free-field listening. II: Psychophysical. *J. Acoust. Soc. Am*, 85(2), 868-878.

- Wightman, F. L., & Kistler, D. J. (1992). The dominant role of low - frequency interaural time differences in sound localization. *The Journal of the Acoustical Society of America*, 91(3), 1648-1661.
- Williams, D. (1992). Cooperative Parallel Processing in Depth, Motion and Texture Perception. In J. R. Brannan (Ed.), *Advances in Psychology* (Vol. 86, pp. 167-225): North-Holland.
- Williams, D., Phillips, G., & Sekuler, R. (1986). Hysteresis in the perception of motion direction as evidence for neural cooperativity. *Nature*, 324(6094), 253-255. doi:10.1038/324253a0
- Winterson, B. J., & Collewyn, H. (1976). Microsaccades during finely guided visuomotor tasks. *Vision research*, 16(12), 1387-1390.
- Wood, C. C. (1974). Parallel processing of auditory and phonetic information in speech discrimination. *Perception & psychophysics*, 15(3), 501-508.
- Wouters, R. J., van den Bosch, W. A., Stijnen, T., Bubberman, A. C., Collewyn, H., & Lemij, H. G. (1995). Conjugacy of eyelid movements in vertical eye saccades. *Investigative Ophthalmology & Visual Science*, 36(13), 2686-2694.
- Wurtz, R. H. (2008). Neuronal mechanisms of visual stability. *Vision Res*, 48(20), 2070-2089. doi:10.1016/j.visres.2008.03.021
- Wurtz, R. H. (2018). Corollary Discharge Contributions to Perceptual Continuity Across Saccades. *Annual review of vision science*, 4, 215-237.
- Wurtz, R. H., & Goldberg, M. E. (1971). Superior colliculus cell responses related to eye movements in awake monkeys. *Science*, 171(3966), 82-84.
- Xia, Y., Leib, A. Y., & Whitney, D. (2016). Serial dependence in the perception of attractiveness. *Journal of vision*, 16(15), 28-28.
- Yantis, S., & Gibson, B. S. (1994). Object continuity in apparent motion and attention. *Canadian Journal of Experimental Psychology/Revue canadienne de psychologie expérimentale*, 48(2), 182-204. doi:10.1037/1196-1961.48.2.182
- Yuan, K.-H., & Maxwell, S. (2005). On the post hoc power in testing mean differences. *Journal of educational and behavioral statistics*, 30(2), 141-167.
- Zee, D. S., Chu, F. C., Leigh, R. J., Savino, P. J., Schatz, N. J., Reingold, D. B., & Cogan, D. G. (1983). Blink - saccade synkinesis. *Neurology*, 33(9), 1233-1233.
- Zee, D. S., & Robinson, D. A. (1979). A hypothetical explanation of saccadic oscillations. *Annals of Neurology: Official Journal of the American Neurological Association and the Child Neurology Society*, 5(5), 405-414.
- Zhang, H., & Alais, D. (2018). Serial dependence for discriminating grating orientation at threshold contrast is driven by perceptual decisions. *Journal of vision*, 18(10), 659-659.
- Zhang, Y., Hedo, R., Rivera, A., Rull, R., Richardson, S., & Tu, X. M. (2019). Post hoc power analysis: is it an informative and meaningful analysis? *General Psychiatry*, 32(4).
- Zhou, W., & King, W. (1998). Premotor commands encode monocular eye movements. *Nature*, 393(6686), 692.
- Zimmermann, E., Burr, D., & Morrone, M. C. (2011). Spatiotopic visual maps revealed by saccadic adaptation in humans. *Current Biology*, 21(16), 1380-1384.
- Zimmermann, M., Meulenbroek, R. G., & de Lange, F. P. (2011). Motor planning is facilitated by adopting an action's goal posture: an fMRI study. *Cerebral Cortex*, 22(1), 122-131.