

BEHAVIORAL AND NEURAL INVESTIGATION ON THE EFFECT OF SPATIAL ATTENTION ON SURROUND SUPPRESSION

A DISSERTATION SUBMITTED TO
THE GRADUATE SCHOOL OF ENGINEERING AND SCIENCE
OF BILKENT UNIVERSITY
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR
THE DEGREE OF
DOCTOR OF PHILOSOPHY
IN
NEUROSCIENCE

By
Merve Kınıklioğlu
September 2023

**Behavioral and Neural Investigation on the Effect of Spatial
Attention on Surround Suppression**

By Merve Kınıklioğlu

September 2023

We certify that we have read this dissertation and that in our opinion it is fully adequate, in scope and in quality, as a dissertation for the degree of Doctor of Philosophy.

Hüseyin Boyacı(Advisor)

H. Hulusi Kafalıgönül

Dicle Dövençioğlu

Buse M. Ürgen

Zahide Pamir Karatok

Approved for the Graduate School of Engineering and Science:

Orhan Arıkan
Director of the Graduate School

ABSTRACT

BEHAVIORAL AND NEURAL INVESTIGATION ON THE EFFECT OF SPATIAL ATTENTION ON SURROUND SUPPRESSION

Merve Kınıklıoğlu

Ph.D. in Neuroscience

Advisor: Hüseyin Boyacı

September 2023

When a visual stimulus is presented together with other stimuli surrounding it, behavioral sensitivity and neural responses may change, often reduce, compared to when the same stimulus is presented alone. This is commonly referred to as center-surround interaction or surround suppression, and it is one of the most fundamental mechanisms in biological vision. It is well documented that in motion perception, center-surround interaction is affected by the size and contrast of the stimulus. As the size of a drifting grating increases, motion direction discrimination performance, as well as neural activity in one of the main cortical motion processing areas, medial temporal complex (MT+), decreases if the grating has high contrast (*surround suppression*). Whereas, when the size increases within certain limits, both the discrimination performance and the neural activity in MT+ may increase if the grating has low contrast (*surround facilitation*). On the other hand, spatial attention is known to modulate surround suppression both in humans and non-human animals with static stimuli. No previous study, however, has directly and systematically investigated the effect of the spatial extent of attention on surround suppression in human motion perception. The studies presented in this dissertation aim to investigate the effect of the extent of spatial attention on center-surround interaction in visual motion processing. In our experiments, we used two attention conditions and a novel stimulus design, where a ‘center’ and a ‘surround’ drifting grating were presented to the participants. Under one of the attention conditions, which we call the ‘narrow-attention’ condition, participants performed a task that limited their attention to the central part of the stimulus. Under the other attention condition, which we call the ‘wide-attention’ condition, participants performed tasks that required them to extend their attention to both the center and surround gratings. Using this experimental paradigm, we measured motion direction discrimination thresholds behaviorally

and cortical activity with fMRI. Behaviorally, we found increased thresholds, that is, stronger surround suppression, under the wide attention condition. In the human homolog of MT+ (hMT+), we found that increasing the spatial extent of attention leads to reduced cortical responses, that is, to stronger neural suppression. This was not the case for the activity in the primary visual cortex (V1). Finally, we show that a parsimonious computational model that incorporates spatial attention and response normalization can successfully predict the response patterns in hMT+ and V1. Furthermore, the model could provide a link between cortical responses and behavioral thresholds. Overall, our findings and analyses showed that the behavioral effect can be successfully predicted by hMT+ activity. These results reveal the critical role of spatial attention on surround suppression, namely that surround suppression in motion perception becomes stronger with a wider attention field, and reveal possible cortical mechanisms underpinning the effect.

Keywords: attention, center-surround interaction, surround suppression, motion perception, normalization, fMRI.

ÖZET

UZAMSAL DİKKATİN ÇEVRESEL BASKILAMAYA ETKİSİNİN DAVRANIŞSAL VE NÖRAL İNCELENMESİ

Merve Kınıkloğlu

Nörobilim, Doktora

Tez Danışmanı: Hüseyin Boyacı

Eylül 2023

Bir görsel uyarın, onu çevreleyen diğler uyarınlarla birlikte sunulduğunda, davranışsal duyarlılık ve nöral tepkiler, aynı uyarının tek başına sunulduğu duruma kıyasla değışebilir ve sıklıkla azalabilir. Bu genellikle merkez-çevre etkileşimi veya çevresel baskılama olarak adlandırılır ve biyolojik görüşteki en temel mekanizmalardan biridir. Hareket algısında merkez-çevre etkileşiminin uyarının boyutundan ve kontrastından etkilendiğı iyi bilinmektedir. Sürüklenen bir ızgaranın boyutu arttıkça, ızgara yüksek kontrasta sahipse ana kortikal hareket işleme alanlarından biri olan medial temporal kompleksteki (MT+) nöral aktivitenin yanı sıra hareket yönü ayırma performansı da azalır (*çevresel baskılama*). Öte yandan, boyut belirli sınırlar dahilinde arttığında, ızgara düşük kontrasta sahipse MT+’ da hem ayırım performansı hem de nöral aktivite artabilir (*çevresel kolaylaştırma*). Buna ek olarak, uzamsal dikkatin hem insanlarda hem de insan olmayan hayvanlarda çevresel baskılamayı statik uyarınlarla modüle ettiğı bilinmektedir. Ancak daha önce yapılan hiçbir çalışma, dikkatin uzamsal kapsamının insan hareket algısında çevresel baskılama üzerindeki etkisini doğrudan ve sistematik olarak incelememiştir. Bu tezde sunulan çalışmalar, görsel hareket işlemede uzamsal dikkatin kapsamının merkez-çevre etkileşimi üzerindeki etkisini araştırmayı amaçlamaktadır. Deneylerimizde, katılımcılara bir ‘merkez’ ve bir ‘çevreleyen’ sürüklenen ızgaranın sunulduğu iki dikkat koşulu ve yeni bir uyarın tasarımı kullandık. ‘Dar dikkat’ koşulu olarak adlandırdığımız dikkat koşullarından birinde katılımcılar, dikkatlerini uyarının orta kısmına sınırlayan bir görev gerçekleştirdiler. ‘Geniş dikkat’ koşulu olarak adlandırdığımız diğler dikkat koşulunda katılımcılar, dikkatlerini hem merkezdeki hem de çevredeki ızgaralara genişletmelerini gerektiren görevler gerçekleştirdiler. Bu deneysel paradigmayı kullanarak, hareket yönü ayırım eşiklerini davranışsal yöntemler kullanarak ve kortikal aktiviteyi (işlevsel magnetik rezonans görüntüleme (iMRG) ile ölçtük. Davranışsal olarak, geniş dikkat koşullarında ayırım eşiklerinin

yükseldiğini, yani daha güçlü bir çevresel baskılama gözlemlendiğini bulduk. MT+'nın insan homologunda (hMT+), dikkatin uzamsal kapsamını arttırmanın kortikal tepkilerin azalmasına, yani daha güçlü nöral baskılamaya yol açtığını bulduk. Ancak, birincil görsel korteksteki (V1) aktivite için bu durum söz konusu değildir. Son olarak, mekansal dikkat ve yanıt normalizasyonunu birleştiren basit bir hesaplamalı modelin, hMT+ ve V1'deki yanıt örüntülerini başarılı bir şekilde tahmin edebildiğini gösterdik. Ayrıca model, kortikal tepkiler ile davranışsal eşikler arasında bir bağlantı sağlayabilmektedir. Genel olarak bulgularımız ve analizlerimiz, davranışsal etkinin hMT+ aktivitesiyle başarılı bir şekilde tahmin edilebildiğini göstermiştir. Bu sonuçlar, mekansal dikkatin çevresel baskılama üzerindeki kritik rolünü, yani hareket algısındaki çevresel baskılamanın daha geniş bir dikkat alanıyla daha güçlü hale geldiğini ve etkiyi destekleyen olası kortikal mekanizmaları ortaya koymaktadır.

Anahtar sözcükler: dikkat, merkez-çevre etkileşimi, çevresel baskılama, hareket algısı, normalizasyon, iMRG.

Acknowledgement

I am grateful to everyone who has sincerely supported me, either in my academic journey or personal life. Thank you for staying by my side and being part of this journey.

First of all, I would like to express my deepest gratitude to my supervisor, Dr. Hüseyin Boyacı, for his continuous support throughout my personal and academic growth and guidance in every aspect of my Ph.D. journey. I learned a lot from his knowledge and expertise, as well as his kindness and patience. I am grateful to him for providing me with a research environment equipped with the necessary resources and opportunities where I can grow into an independent researcher.

I would like to express my special gratitude to Dr. Hulusi Kafalgönül for his continuous support, valuable advice, and sharing his experiences and guidance on several aspects of academia and life. Also, I would like to thank Dr. Dicle Dövençioğlu, Dr. Zahide Pamir and Dr. Buse M. Ürgen for their valuable contributions and feedback.

I would like to thank my lab members, Amna Malik, and Dilara Erişen for their sincere support, intellectual contributions to my research, and valuable companionship. Also, I would like to thank other members of CBVG, as well as my UMRAM friends, Tuğçe Çabuk, Efsun Kavaklıoğlu, Samet Albayrak for their intellectual and moral support during my PhD. I am thankful to all of them for making the workplace a fun and enjoyable environment.

I would also like to thank my academic mom, Sibel Akyüz, for her sincere support and invaluable guidance. Our late-night work sessions at Umram will be sorely missed. I want to thank the best neighbor, both in the office and at home, Esra Çatak, for her comforting presence and warm-hearted support.

I don't think I could manage to come this far without Afife Konyalı Türker and Didenur Şahin Çevik in my life. Thank you for being by my side through every high and low, for sharing in my joys and comforting me in my sorrows. Your unwavering presence means the world to me.

Finally, I am forever grateful for my family, Afife, Şakir, Süleyman, Mehmet and Seda for their continuous support and encouragement in every way. It is

impossible to express what their belief in me, comforting presence, and unconditional support mean to me. I would like to thank Öznur Satılmışoğlu for always supporting me and being there every time I needed her. I would also like to thank my grannies, Ayşe and Nafize for all the love and prayers for my success and sanity.

Finally, I would like to acknowledge the financial support provided by the Scientific and Technological Research Council of Turkey (TUBITAK BİDEB 2211 Program, 2211 BİDEB National Graduate Scholarship Program).



I would like to dedicate this dissertation to the most hardworking, incredibly selfless and powerful woman I know, my mom Afife, as well as all women in this odd planet who run with the wolves.

Le vent se lève! il faut tenter de
vivre!

The wind is rising! We must try
to live.

Paul Valéry



Contents

1	Introduction	1
1.1	Human Visual System	2
1.2	Surround Suppression	9
1.3	Spatial Attention	18
1.3.1	Spatial Attention and Changes in Visual Responses	20
1.3.2	Normalization Model of Attention	23
1.4	Spatial Attention and Surround Suppression	28
1.5	Current Study	30
2	Behavioral Experiment	34
2.1	Introduction	34
2.2	Methods	36
2.2.1	Participants	36
2.2.2	Apparatus	36
2.2.3	Stimuli and Design	36
2.2.4	Data Analysis	39
2.3	Results	40
2.4	Discussion	46
3	fMRI Experiment	51
3.1	Introduction	51
3.2	Methods	53
3.2.1	Participants	53
3.2.2	Psychophysics	53
3.2.3	fMRI	57

3.2.4	Data Analysis	62
3.3	Results	65
3.3.1	Behavioral Results	65
3.3.2	fMRI Results	66
3.3.3	Comparing Behavioral and fMRI Results	69
3.4	Discussion	72
4	Computational Modeling	76
4.1	Introduction	76
4.2	Methods	77
4.3	Results	82
4.3.1	Model Results for Behavioral Experiment	82
4.3.2	Model Results for the fMRI Experiment	82
4.4	Discussion	86
5	General Discussion and Future Directions	87
5.1	Wider spatial attention leads to stronger surround suppression . .	89
5.2	Activity of hMT+ neurons better captures the perceptual effect .	90
5.3	Spatial attention has a weaker effect when center and surround move in the opposite direction	91
5.4	Clinical populations, surround suppression, and spatial attention .	92
5.5	Normalization model of attention can explain the results	93
5.6	Limitations and Future Directions	94
5.7	Conclusion	96
A	Psychometric Function Fits in Behavioral Experiments	97
B	Permissions to Re-use Figures	128

List of Figures

1.1	Simplified illustration of the connections, cell types, and layers in the retina. Electrical signals from the photoreceptors (rods and cones) are relayed to the optic nerve through interneurons such as bipolar cells, horizontal cells, and amacrine cells. Then, axons of the ganglion cells form the optic nerve, leave the retina, and convey neural information to the LGN and the visual cortex. Reprinted, with permission, from ref. [1]. See Appendix.	3
1.2	Illustration of the Parvo-dominated ventral pathway and Magno-dominated dorsal pathway, starting from the retina to higher-visual areas. Reprinted, with permission, from ref.[2]. See Appendix. . .	7
1.3	Example stimulus set that is frequently used in human surround suppression research. The size of the stimulus changes from small (1.5°) to medium (4°) and large (8°) from left to right. The contrast of the stimulus changes from high contrast (98%) to medium (50%) and low contrast (5%) from top to bottom.	12
1.4	Example stimulus set that is frequently used in surround suppression animal research. The red circle represents the receptive field (RF) of the neuron. The first row illustrates the center grating that covers RF and annular gratings varying in size from small to medium and large surrounds, which are located at various distances from the center grating. The second row illustrates the center grating that covers RF and annular grating, varying in size from small to medium and large surround.	13
1.5	Example stimuli with different spatial frequencies (left to right: 1 cycle per degree (cpd), 2 cpd, and 4 cpd).	15

1.6	Typical effect of size-contrast interaction in motion perception. Left: Motion direction discrimination thresholds. As the size of a drifting grating increases, motion direction discrimination thresholds increase for high-contrast stimuli and decrease for low-contrast stimuli. Right: Suppression Index (SI) values. The suppression index quantifies the strength of the surround suppression. Higher positive SI values for high contrast indicate surround suppression, whereas negative SI values for low contrast indicate surround facilitation.	16
1.7	Illustration of contrast response functions for a stimulated neuron for response gain and contrast gain. Response gain is typically characterized as an upward shift of the contrast-response function, whereas contrast gain is typically characterized as a leftward shift of the contrast-response function [3, 4]	22
1.8	A schematic representation of the normalization model. The Excitatory Drive is normalized by the Suppressive Drive to determine population response (see Equation 1.2).	24
1.9	A schematic representation of the normalization model of attention. Stimulus Drive is multiplied by the attention field, then normalized by the Suppressive Drive to determine population response (see Equation 1.3).	26
2.1	Center-only, small-surround, and large-surround configurations for high (98%) contrast stimuli.	37
2.2	Experimental design for the narrow and wide attention conditions. Participants were asked to keep their eyes on a fixation point throughout the trial. Each trial began with a fixation point followed by the presentation of the stimulus, whose duration was adjusted with two interleaved 1-up 3-down staircases. In the narrow attention condition, participants reported the motion direction of the center grating. In the wide attention condition, participants first reported the drift direction of the central grating, then reported whether the central and annular gratings drifted in the same direction.	39

2.3	Behavioral results. Motion direction discrimination thresholds averaged across participants. A and B for same direction trials, C and D for opposite direction trials. Error bars represent SEM.	42
2.4	Suppression Indices (SI). A and B, same direction trials, C and D, opposite direction trials. Higher values of <i>SI</i> indicate stronger surround suppression, and negative <i>SI</i> values indicate surround facilitation. Symbols represent individual participants, and the red and blue lines show averages for narrow and wide attention conditions, respectively. Error bars represent SEM.	43
3.1	Center-only, and center+surround configurations.	54
3.2	Trial sequence for the narrow and wide attention conditions in the behavioral tests conducted before fMRI scans. Participants were asked to fixate on the center of the display throughout the trial. Each trial began with a fixation point followed by the presentation of the stimulus, whose duration was adjusted with two interleaved 1-up, 3-down staircases. In the narrow attention condition, participants reported the motion direction of the center grating. In the wide attention condition, participants first reported the drift direction of the central grating, then reported whether the central and annular gratings drifted in the same direction.	55
3.3	Schematic depiction of mixed blocked/event-related design of the fMRI experiment. In the paradigm, task blocks were alternated with rest blocks. The order of two block types (NA: narrow attention; WA: wide attention) was randomly determined. The narrow attention block consisted of center-only, same- and opposite-direction trials. Wide attention blocks consisted of same- and opposite-direction trials. Within each task block, trials were jittered with ITIs ranging from 4 to 8 s.	58

3.4	Trial sequence of the narrow- and wide-attention blocks in the functional run. Participants were asked to fixate on the center of the display throughout the trial. At the beginning of the each block, instruction for the task was written on the instruction screen in detail. In the narrow attention block, the participants were instructed to attend only to the center grating and report its motion direction. In the wide attention block, the participants were instructed to attend both center and surround gratings and report whether the central and annular gratings drifted in the same direction. Each trial began with a fixation point, followed by the presentation of the stimulus for 150 ms. In the real experiment, the possible answers were not written on response screen.	59
3.5	Analysis pipeline.	60
3.6	Location of the representative hMT+ and V1 ROIs on the inflated surface.	63
3.7	Behavioral results. Left: Motion direction discrimination thresholds averaged across participants. Right: Suppression Indices (SI). Higher values of <i>SI</i> indicate stronger surround suppression and negative <i>SI</i> values indicate surround facilitation. Symbols represent individual participants, and the red and blue lines show averages for narrow and wide attention conditions, respectively. * indicates significance at $p < 0.05$. Error bars represent SEM. . . .	67
3.8	hMT+ results. Left: Beta values extracted from averaged across participants. Right: Suppression Indices (SI) derived from beta values. Red and blue lines indicate narrow and wide attention conditions, respectively. * indicates significance at $p < 0.05$. Error bars represent SEM.	68
3.9	V1 results. Left: Beta values extracted from averaged across participants. Right: Suppression Indices (SI) derived from beta values. Red and blue lines indicate narrow and wide attention conditions, respectively. Error bars represent SEM.	69

3.10	Sensitivity values (1/duration threshold). Red and blue lines show averages for narrow and wide attention conditions, respectively. Error bars represent SEM.	70
3.11	Relationship between the effect of attention, defined as the difference in SIs between narrow and wide attention conditions (i.e. Attention Index; AI), observed in fMRI hMT+ and behavioral experiment.	71
3.12	Relationship between the effect of attention, defined as the difference in SIs between narrow and wide attention conditions (i.e. Attention Index; AI), observed in fMRI V1 and behavioral experiment.	71
4.1	A schematic representation of the normalization model of attention. Stimulus Drive is multiplied by the attention field, then normalized by the Suppressive Drive to determine population response. We simulated model responses using a narrow attention field for the narrow attention condition (red dashed squares) and a wider attention field for the wide attention condition (blue dashed squares) (Eqs. 4.1- 4.3).	79
4.2	Model simulation results for behavioral experiment based on parameters from MT neurons. Predictions of the normalization model for the same-direction trials (A and B) and opposite-direction trials (C and D).	83
4.3	Model simulation results for the pre-fMRI behavioral experiment. Predictions of the normalization model for the same- and opposite-direction trials, based on parameters from MT neurons.	84
4.4	Model results for the fMRI BOLD response based on parameters that characterize MT neurons.	85
4.5	Model results for the fMRI BOLD response in V1 based on parameters that characterize V1 neurons.	85
A.1	Weibull function fits for a single participant (1) for center-only condition.	98

A.2	Weibull function fits for a single participant (1) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	98
A.3	Weibull function fits for a single participant (1) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	99
A.4	Weibull function fits for a single participant (2) for center-only condition.	99
A.5	Weibull function fits for a single participant (2) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	100
A.6	Weibull function fits for a single participant (2) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	101
A.7	Weibull function fits for a single participant (3) for center-only condition.	101
A.8	Weibull function fits for a single participant (3) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	102
A.9	Weibull function fits for a single participant (3) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	103
A.10	Weibull function fits for a single participant (4) for center-only condition.	103

A.11 Weibull function fits for a single participant (4) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	104
A.12 Weibull function fits for a single participant (4) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	105
A.13 Weibull function fits for a single participant (5) for center-only condition.	105
A.14 Weibull function fits for a single participant (5) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	106
A.15 Weibull function fits for a single participant (5) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	107
A.16 Weibull function fits for a single participant (6) for center-only condition.	107
A.17 Weibull function fits for a single participant (6) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	108
A.18 Weibull function fits for a single participant (6) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	109
A.19 Weibull function fits for a single participant (7) for center-only condition.	109

A.20	Weibull function fits for a single participant (7) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	110
A.21	Weibull function fits for a single participant (7) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	111
A.22	Weibull function fits for a single participant (8) for center-only condition.	111
A.23	Weibull function fits for a single participant (8) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	112
A.24	Weibull function fits for a single participant (8) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	113
A.25	Weibull function fits for a single participant (9) for center-only condition.	113
A.26	Weibull function fits for a single participant (9) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	114
A.27	Weibull function fits for a single participant (9) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	115
A.28	Weibull function fits for a single participant (10) for center-only condition.	115

A.29 Weibull function fits for a single participant (10) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	116
A.30 Weibull function fits for a single participant (10) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.	117
A.31 Weibull function fits for a single participant (1) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.	118
A.32 Weibull function fits for a single participant (2) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.	119
A.33 Weibull function fits for a single participant (3) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.	120
A.34 Weibull function fits for a single participant (4) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.	121
A.35 Weibull function fits for a single participant (5) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.	122
A.36 Weibull function fits for a single participant (6) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.	123

A.37 Weibull function fits for a single participant (7) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.	124
A.38 Weibull function fits for a single participant (8) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.	125
A.39 Weibull function fits for a single participant (9) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.	126
A.40 Weibull function fits for a single participant (10) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.	127

List of Tables

2.1	Results of one-sample t -test for same-direction trials ($H_0 : SI = 0$). Numbers in degrees are the surround diameters.	41
2.2	Results of three-way ANOVA for same direction trials.	44
2.3	Results of one-sample t -test for opposite-direction trials ($H_0 : SI =$ 0). Numbers in degrees are the surround diameters.	45
2.4	Results of three-way ANOVA for oopposite direction trials.	46
4.1	Normalization model parameters for simulating behavioral results.	81
4.2	Normalization model parameters for simulating fMRI results. . . .	81

Chapter 1

Introduction

This thesis focuses on investigating the effect of spatial attention on surround suppression in motion perception. To achieve this goal, it is necessary to consider the underlying mechanisms that give rise to surround suppression and motion perception. The following sections focus on the retinal and neural circuitry that play a crucial role in these phenomena. Specifically, I will explore how visual signals from the retina are transmitted to the brain and how they are processed in the striate and extrastriate cortex via specialized neurons along distinct neural pathways. Furthermore, this chapter will examine the current literature on spatial attention and surround suppression. I will review different theories and models proposed to explain the neural mechanisms underlying these phenomena. Moreover, I will discuss the role of surround suppression in motion perception and how it is affected by attentional mechanisms. By thoroughly examining these topics, I aim to shed light on the complex interplay between spatial attention and surround suppression in motion perception. Finally, I will describe the scope and motivation of the present study. Then, in the following chapters, I will provide empirical evidence for the effect of spatial attention on surround suppression in human motion perception and discuss the implications and potential applications of these findings for our understanding of attentional mechanisms in surround suppression.

1.1 Human Visual System

Vision is the most complex and frequently studied sensory modality across all sensory systems [5]. It is partly because we rely on vision more than other senses while interacting with the world [6]. Furthermore, a large amount of neural circuitry is dedicated to processing visual information [7], and more than 50% of the mammalian cerebral cortex contributes to it [8, 9].

Visual information processing begins at the retina when light reflected from objects enters the eye. The retina, a layer at the back of the eye, contains various cell types specialized for visual information processing, such as photoreceptors (rods and cones), bipolar, amacrine, horizontal, and ganglion cells [10]. Light is transduced into neural activity by photoreceptors located in the inner parts of the retina. Specifically, when light enters the retina, photoreceptors undergo a cascade of events that leads to hyperpolarization of the cell, through which light energy is converted into chemical energy [11, 12].

There are two types of photoreceptors: rods and cones. Cones are color selective and responsible for highly detailed, sharp vision at the fovea, whereas rods are sensitive to dim light and responsible for less detailed night vision at the periphery.

The photoreceptor density varies greatly for different parts of the retina. The cones are densely located at the fovea, a part of the retina where visual acuity is highest. There is less convergent circuitry in the fovea as most photoreceptors have a one-to-one relationship with ganglion cells which leads to sharp vision. The rod photoreceptor density is very high in the periphery, whereas only a few cones are located there. Periphery has a highly convergent circuitry where a ganglion cell receives input from more than one photoreceptor, which leads to highly sensitive peripheral vision [13].

Electrical signals from the photoreceptors are relayed to the optic nerve through interneurons such as bipolar cells, horizontal cells, and amacrine cells

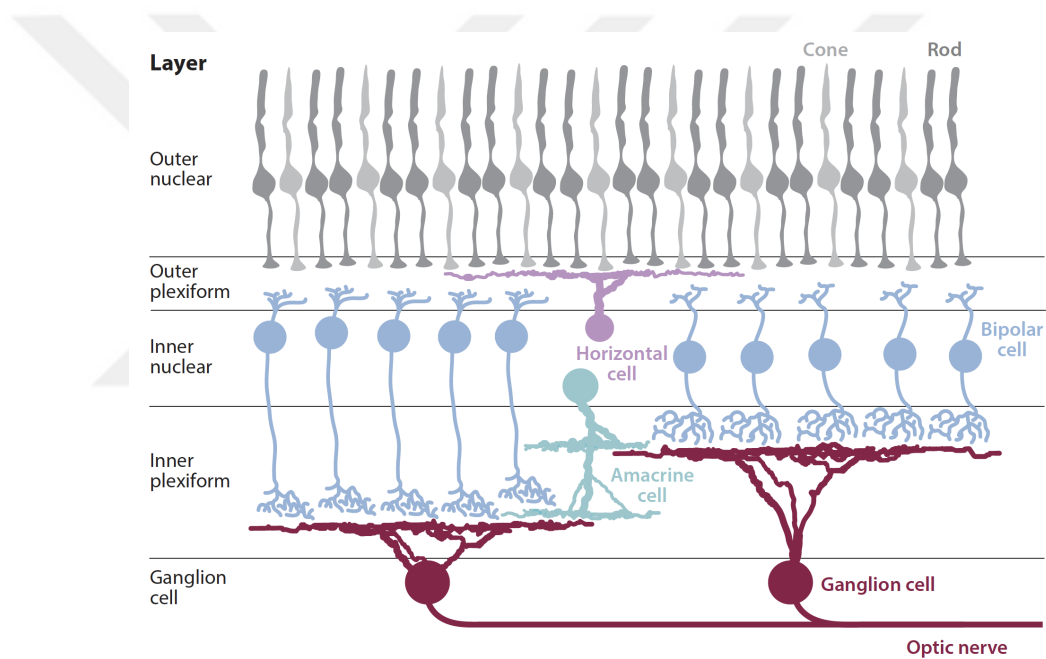


Figure 1.1: Simplified illustration of the connections, cell types, and layers in the retina. Electrical signals from the photoreceptors (rods and cones) are relayed to the optic nerve through interneurons such as bipolar cells, horizontal cells, and amacrine cells. Then, axons of the ganglion cells form the optic nerve, leave the retina, and convey neural information to the LGN and the visual cortex. Reprinted, with permission, from ref. [1]. See Appendix.

[10]. Specifically, horizontal cells integrate the information from the photoreceptors and convey it to bipolar cells. Bipolar cells are divided into two types based on their responses to light: ON- and OFF-bipolar cells. ON-bipolar cells depolarize in response to light, whereas OFF-bipolar cells hyperpolarize. Bipolar and amacrine cells transmit information from photoreceptors to retinal ganglion cells (RGC).

The receptive field (RF) of a neuron is a part of the visual field where the presentation of stimuli elicits a change in the response of that neuron [14]. RGCs typically have center-surround receptive field organization and also show on- and off-response patterns to light depending on the input from different types of bipolar cells [15]. Specifically, the center and surround regions of receptive fields respond oppositely to light. For example, the firing rate of the on-center, off-surround ganglion cell (ON-cell) increases when light is presented only to the center of the RF, whereas it decreases when the light is presented in the RF surround. In a similar sense, the firing rate of the off-center on-surround ganglion cell (OFF-cell) increases when the RF surround is illuminated, and its response decreases when the light is presented in the RF center. Related to that, response of a neuron to a stimulus is suppressed by the excitation of a neighboring neuron, which is called lateral inhibition [16]. Lateral inhibition is important for refining sensory information as it increases sensitivity to spatially variant stimuli [17, 18].

Finally, axons of the retinal ganglion cells form the optic nerve, leave the retina, and convey neural information to the lateral geniculate nucleus (LGN) and the visual cortex. Retinal ganglion cells are also categorized into two main groups based on their morphology, response profile, and pathways they construct: M-parasol cells and P-midget cells. P cells (also known as midget cells) have smaller cell bodies and fewer/shorter dendrites compared to M cells. They constitute 95% of the retinal ganglion cells. P cells have smaller receptive fields and have a more sustained response profile to a prolonged visual stimulus. They are highly sensitive to color and spatial frequency and mainly contribute to shape and color perception. P cells dominantly project to the parvocellular (dorsal) layer of the LGN and later construct the parvocellular pathway. M cells have more dendrites

and larger receptive fields, and they are less sensitive to color while highly sensitive to low-contrast stimuli. They have a more transient response profile and faster conduction to a prolonged visual stimulus. M cells dominantly project to the magnocellular (lateral) layer of LGN and, later on, construct the magnocellular pathway. They are mainly involved in motion and depth perception. There are also cells projecting to the koniocellular layer of LGN, which is located between the parvocellular and magnocellular layers, and they are involved in color perception.

At the optic chiasm, nerve fibers that come from the nasal retina cross over to the other side of the brain and connect with axons that come from the temporal retina of the other eye. Together, these contralateral and ipsilateral axons give rise to the optic tract, which propagates to LGN in the thalamus. LGN is the main relay station for visual information, as it converges the afferent sensory signals coming from retinal ganglion cells and transmits them to the primary visual cortex (V1). However, more than being a simple feedforward relay station in the visual pathway, LGN has a more intricate role in visual processing as it also receives cortical feedback projections. Therefore, the activity of the LGN is not solely determined by bottom-up sensory input, as top-down cognitive processes such as attention also influence its activity [19, 20].

LGN consists of six layers. The top four LGN layers constitute the parvocellular pathway (P pathway), which mainly receives inputs from the P-midget cells, whereas the bottom two LGN layers form the magnocellular pathway (M pathway), which mainly receives input from M-parasol cells. The M and P pathways complement each other, and these segregated projections later form the dorsal and ventral pathways that go beyond V1. Similar to ganglion cells, LGN also has center-surround receptive field organization.

Axons from the LGN give rise to the optic radiations, which project to the primary visual cortex (V1). Due to tissue characteristics, the primary visual cortex is also called the striate cortex. The primary visual cortex maintains the segregated organization through projections from the LGN (e.g., M and P pathways) [21]. Similar to the structure of LGN, V1 also has a layered structure.

Magnocellular layers of LGN project signals to $4C\alpha$ and $4B$ layers of V1, whereas parvocellular layers send signals to the $4C\beta$ layer of V1.

V1 neurons are highly sensitive to certain stimulus features like orientation, motion direction, color, and binocular disparities [22, 23, 24, 25, 26]. Besides, V1 has columnar organization. For example, there are location columns perpendicular to the surface, in which neurons that have their RF at about the same location cluster together. Within a location column, there are also orientation columns in which neurons that tune to a specific orientation cluster together [23, 27]. There are also ocular dominance columns, where neurons receiving input from the same eye are grouped together. Finally, neurons that are selective to color and low-frequency information are located in color blobs (CO) of V1 [28].

V1 transmits visual information to higher visual areas through two major pathways: the dorsal and ventral pathways, which mainly process different aspects of visual information [29]. In the dorsal (parietal) pathway, also called magnocellular-dominated or where/how pathway, V1 neurons mainly receive information from magnocellular neurons and project along to the parietal lobe, including thick stripes of V2, dorsal V3 (V3d), V3 A/B, V5 (MT; medial temporal area), and MST (medial superior temporal). It mainly processes direction and speed of motion and is tuned for binocular disparity. The dorsal pathway plays a critical role in motion and depth perception. It also contributes to visually guided actions by processing the visuospatial properties of the object and transforming them into suitable motor actions [30].

MT is the central processing stage along the dorsal pathway and has a crucial role in motion perception, which is the topic of the current thesis. Indeed, lesion and stimulation studies showed that disrupting MT activity leads to deterioration in motion perception [31, 32, 33]. MT neurons show selectivity for direction and speed of motion as well as binocular disparity [34, 35, 36, 37]. Similar to orientation columns in V1, MT neurons tuned to specific motion directions are grouped together on the surface of MT. There is also evidence for a clustered organization of speed tuning within MT [38]. MT neurons have (approximately ten times) larger receptive fields compared to V1 neurons, which enables them

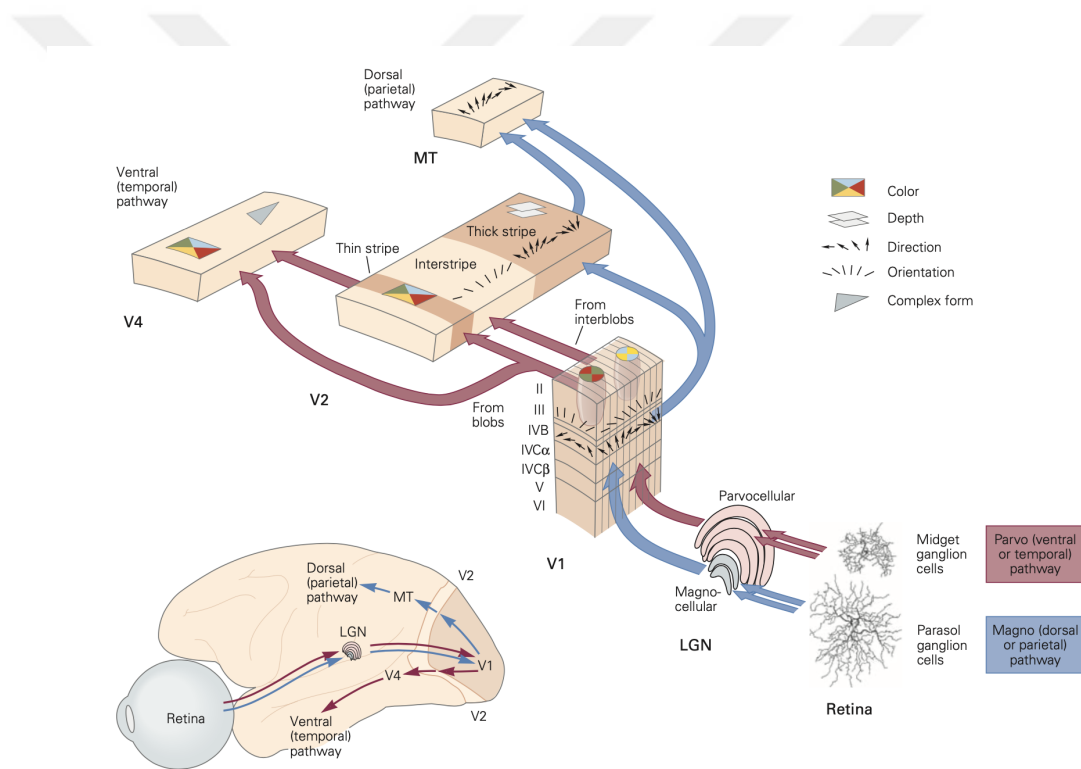


Figure 1.2: Illustration of the Parvo-dominated ventral pathway and Magno-dominated dorsal pathway, starting from the retina to higher-visual areas. Reprinted, with permission, from ref.[2]. See Appendix.

to have motion integration [39, 40, 41]. Specifically, MT neurons integrate local motion signals coming from V1 neurons into global motion to determine the overall direction of the stimuli [42].

MST, located anterior to the MT region, also plays a role in motion processing. MST neurons have even larger receptive fields to encode more complex motion signals such as expansion and contraction [43]. They are highly selective for binocular disparity and optic flow [44, 45]. MST neurons are also involved in the integration of visual and vestibular information during the movement of the observer [46]. MT and MST are collectively called MT+, as both mainly contribute to motion perception [47, 48].

On the other hand, in the ventral (temporal) pathway, which is also called the parvocellular-dominated or the ‘what pathway,’ V1 neurons mostly get information from parvocellular neurons and send out projections along the temporal cortex, including thin and pale stripes of V2, ventral V3, V4, and IT (inferior temporal cortex). It mainly processes color and shape information and contributes to object and face recognition [18].

Note that even though well-characterized hierarchical information flow is observed in the visual system, there are also feedback connections coming from higher-level areas. Interestingly, there are much more feedback connections than feedforward inputs in visual processing [19], which suggests that these connections play an important role in visual perception. One of the primary functions of feedback connections in visual processing is attentional and contextual modulation [49]. For example, there is evidence of both excitatory and inhibitory feedback projections from higher visual areas to the earlier visual areas, which contributes to contextual modulation of neural responses in the visual cortex, the integration of information, shaping receptive field properties, and the refinement of visual representations [50, 51, 52].

Importantly, there is also neural evidence suggesting that cortico-cortical feedback circuits transmit top-down attention signals to lower visual areas [53, 54, 55, 56, 57]. For example, feedback connections from the middle temporal

area (MT), frontal eye fields (FEF), and intraparietal sulcus (IPS) enhance the responses of neurons in lower visual areas, including V1 and V2, and contribute to the selective processing of attended visual stimuli [58, 59, 60]. These feedback connections play a crucial role in top-down control, biasing sensory processing in favor of attended stimuli and integrating cognitive and sensory signals for selective attention. Although the attentional modulation of the visual responses is well-documented [19], there are still unanswered questions regarding the specific functional contributions of the top-down attention signals to visual processing.

1.2 Surround Suppression

Due to the antagonistic center-surround organization of the receptive field, a neuron's responses to a stimulus presented at the center of its receptive field are suppressed by stimuli presented in its surround [61, 62]. Such an effect is called surround suppression, and it is observed when the stimuli are presented in the neuron's extra-classical receptive field (eCRF) [50, 63], which is a part of the visual field where the stimuli cannot evoke a firing response but can modulate the response to a stimulus in the classical receptive field (CRF) which is a part of the visual field where the presentation of stimuli elicits a change in the response of that neuron [14]. While surround suppression is first examined at the single-unit level, its effects are more extensively manifested in the activity of population of neurons [64, 65]. This is particularly important because the processing and perception of sensory information typically involve the coordinated activity of neuronal populations rather than isolated units [66, 67].

Surround suppression is observed in many species, such as cats, humans, monkeys, and mice; and in sensory systems, including auditory [68, 69], somatosensory [70, 71], and olfactory systems [72]. Importantly, surround suppression is particularly well characterized in the vision as it is observed at many levels of the visual system [65], including the retina [73, 74], superior colliculus [75, 76], lateral geniculate nucleus (LGN) [77, 78, 79, 80, 81], striate or primary visual cortex (V1), [82, 61, 83, 84, 85, 86, 87] and extrastriate cortex [88, 89, 90].

Surround suppression mainly contributes to edge detection, figure-ground segregation, contour integration, perceptual grouping, and motion detection [65]. Furthermore, the efficient coding theory suggests that natural images have temporal and spatial correlations that contain redundant information [91, 92], and surround suppression may also play a role in suppressing redundant signals to emphasize more informative regions like edges and enhance the sparseness of the response. Experimental evidence suggests that surround suppression is indeed involved in redundancy reduction and refinement of sensory information [93, 94, 95].

Surround suppression is typically investigated with full sinusoidal gratings presented in different size levels (mostly in population level [96, 97, 98, 99, 64, 100, 101, 102], see Figure 1.3) or center grating that covers RF and annular grating varying in size (mostly in single-unit level [82, 50, 61, 65, 103, 104, 105], see Figure 1.4). Early studies showed that surround suppression is highly affected by stimulus parameters and contextual factors [65]. For example, surround suppression is spatially extensive. Although the strength of surround suppression in V1 decreased with increasing distance from the center of the receptive field, it is still observed up to 12.5 degrees away from the RF center [61, 65]. Besides, the magnitude of suppression increases when the center and surround have the same orientation, spatial frequency, drift direction, and speed. Furthermore, surround suppression is strongest for iso-oriented stimuli, regardless of the orientation preference of neurons [65].

There are many studies in the literature that aim to characterize the classical and extraclassical RF sizes in the visual cortex to understand the dynamics of surround modulation. These studies often use a combination of neurophysiological recordings and visual stimuli to map the receptive field properties of individual neurons [50]. Researchers typically use high-contrast gratings with varying sizes to find the extent of the area over which responses summate, which is CRF, and the extent of the classical receptive field surround. The typical CRF size in V1 is around 1 degree $\pm$ 0.01 at 2 to 8 degrees of eccentricity, and its surround size is around 5.1 degree $\pm$ 0.06, ranging up to 28 degrees [50, 106, 107, 108]. MT neurons have approximately ten times larger receptive fields compared to V1 neurons, and the receptive fields of MT neurons span from a few degrees to over

20 degree depending on the specific location within MT and the distance from the fovea [39].

The size and contrast of the stimuli also affect surround suppression. As the stimulus size increases, the strength of surround suppression also increases for high contrast [61, 109, 110, 111, 112]. However, when the stimuli are presented in low contrast, increasing the stimulus size results in weaker suppression [61, 105, 113, 114] or sometimes surround facilitation [103, 112]. Surround facilitation is characterized as an increase in neural response when the stimulus is presented at the extra-classical RF [62, 103, 115].

In this thesis, we will focus on surround suppression in the V1 and MT areas that are involved in motion perception. As stated previously, surround suppression is well documented both in V1 and MT [65]. For example, single-unit recording studies in animal models showed that the spike rate of a neuron in V1 decreases when a stimulus is presented both within and outside of its classical receptive field, compared to when a stimulus falls only within its classical receptive field [82, 61, 103, 104, 109, 116]. Similar effects of surround suppression were also observed for MT neurons at the single-unit level in animal models. When a drifting stimulus is presented simultaneously in both the center and surround parts of the receptive field, the neuron’s firing rate is reduced or suppressed [117].

Neurophysiology studies suggest that visual perception is mediated by a population of neurons rather than by single neurons [66, 67]. Therefore, even though surround suppression is initially studied at the single unit level, the effect at the population level also needs to be characterized to fully understand this phenomenon. To do so, researchers used various methods, including functional magnetic resonance imaging (fMRI), electroencephalogram (EEG), transcranial magnetic stimulation (TMS), and magnetoencephalography (MEG), to examine surround suppression at the population level in humans as well as non-human animals.

At population-level, however, as it is hard to talk about the RF center and surround, instead the frequently used stimulus usually consists of a central part,

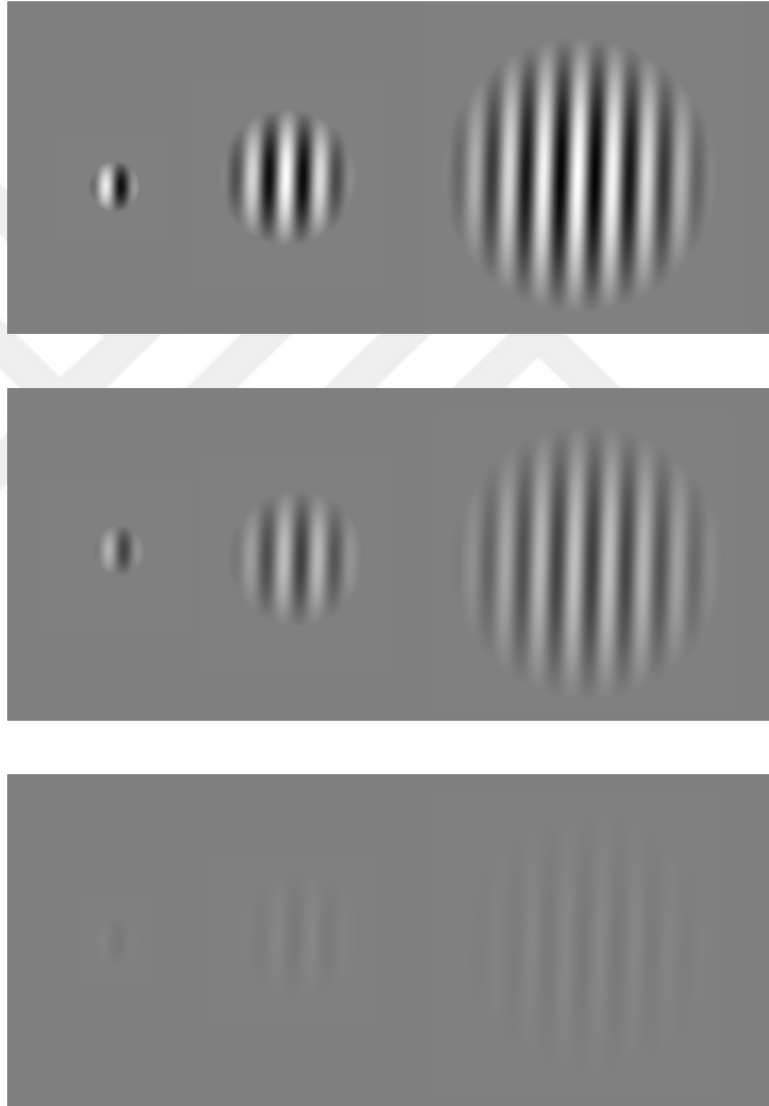


Figure 1.3: Example stimulus set that is frequently used in human surround suppression research. The size of the stimulus changes from small (1.5°) to medium (4°) and large (8°) from left to right. The contrast of the stimulus changes from high contrast (98%) to medium (50%) and low contrast (5%) from top to bottom.

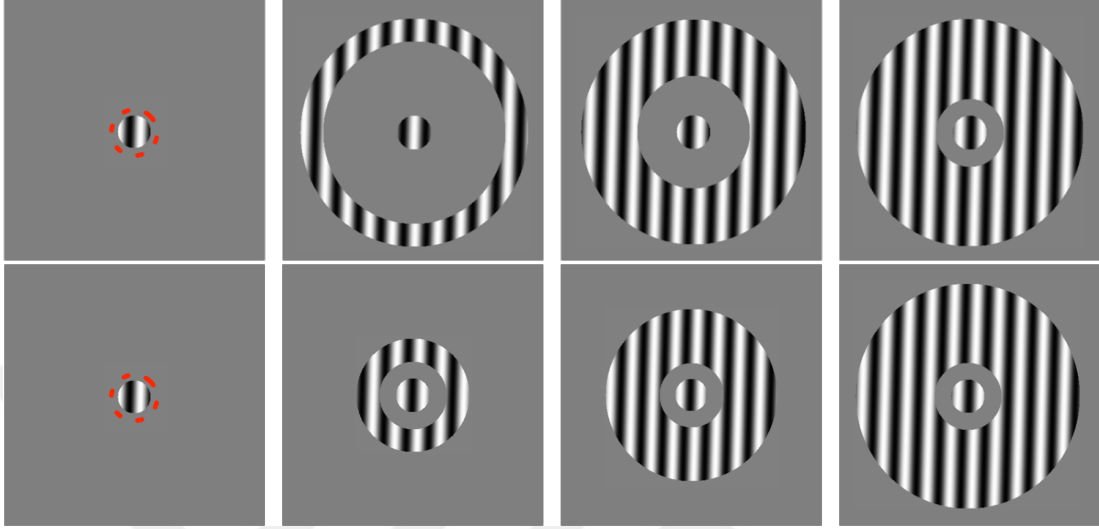


Figure 1.4: Example stimulus set that is frequently used in surround suppression animal research. The red circle represents the receptive field (RF) of the neuron. The first row illustrates the center grating that covers RF and annular gratings varying in size from small to medium and large surrounds, which are located at various distances from the center grating. The second row illustrates the center grating that covers RF and annular grating, varying in size from small to medium and large surround.

which is also called the target stimulus [118, 119, 120], presented with a surround part, which is also called the neighboring stimulus [121] or flanking stimulus [122, 123] even called mask in certain studies [118, 119, 120]. These stimuli enable us to investigate the modulatory effect of surrounding stimuli on the central stimulus. Findings of studies that used such stimuli to investigate surround suppression at the population level revealed an analogous suppression effect. For example, neural responses in humans measured by functional magnetic resonance imaging show a pattern of results similar to those at the single-unit level: BOLD responses in V1 decrease when a central stimulus is presented with a surround compared to when it is presented alone [124, 125, 126, 127]. Likewise, presenting a central stimulus with a surrounding stimulus, led to reduced activity in early visual areas, including V1, V2, and V3 [128]. Moreover, the studies investigating surround suppression in the cat [129, 130], and macaque visual cortex [131] using fMRI found that presenting a center stimulus together with a surrounding stimulus resulted in decreased activity in V1 and higher visual areas. They also observed that the suppressive effects were more pronounced when the center and surround

stimuli had similar orientations.

Similar effects of surround suppression were also observed for MT neurons in human fMRI studies. Specifically, fMRI response to a center stimulus was reduced when presented with a surrounding annular stimulus, indicating the presence of surround suppression in the MT area. Besides, stronger suppression effects were observed in human MT when the surround stimuli were larger and presented in high contrast compared to low contrast [96, 97, 98].

On the other hand, EEG studies that investigate surround suppression in the visual cortex often show that early visual evoked potentials, such as the P1 and N1 components, are reduced in response to a center stimulus when it is surrounded by a high-contrast annular stimulus [132]. Besides, higher contrast and spatially contiguous surrounds were found to induce stronger suppression effects [133, 121, 134]. Similarly, MEG responses in the visual cortex decreased in response to presenting a center stimulus along with a surround stimulus. This reduction indicates the presence of surround suppression in the MEG signals. Besides, this suppression was stronger for higher contrast iso-oriented surrounds [135, 136]. Moreover, TMS-induced disruption of the visual cortex also affects surround suppression. For example, disrupting hMT activity with TMS resulted in decreased surround suppression for high-contrast stimuli [101].

Similar to the neural effect of surround suppression, there is a well-documented perceptual effect in human motion perception: as the size of a drifting grating increases, discriminating the motion direction of the grating becomes harder. This means that for high contrast, motion direction discrimination thresholds, which are the minimum amount of time needed to correctly decide the direction of motion, increase. On the contrary, as the size of a drifting grating increases, motion direction discrimination thresholds decrease for low contrast stimuli [64] (see Figure 1.6). These findings have been consistently observed in numerous studies [96, 97, 98, 99, 64, 101, 137, 138, 139] which makes it a well-known visual paradigm to study surround suppression in human motion perception. Furthermore, many studies in the literature used the Suppression Index (SI) to quantify the strength of the surround suppression. SI is typically calculated with the



Figure 1.5: Example stimuli with different spatial frequencies (left to right: 1 cycle per degree (cpd), 2 cpd, and 4 cpd).

following equation:

$$SI = \frac{T_{large} - T_{small}}{T_{small}} \quad (1.1)$$

where T_i is the discrimination threshold for a given size. Higher positive SI values indicate stronger surround suppression, whereas negative SI values mean surround facilitation. An SI of 0 means no suppression or facilitation.

Such perceptual effects have been explained by the surround suppression mechanism arising from antagonistic center-surround interactions of the neural populations in the middle temporal cortex (MT) [64]. Indeed, this MT hypothesis is supported by previous studies showing that there is a high correspondence between behavioral thresholds and MT activity. To be more specific, MT activity decreases with stimulus size at high contrast, parallel to a decrease in performance in the direction discrimination task, whereas it increases with stimulus size at low contrast, parallel to increases in performance [96, 97, 99]. Furthermore, disrupting hMT+ activity with TMS resulted in decreased surround suppression for high-contrast stimuli [101]. Although these findings support the MT hypothesis, similar effects of surround suppression were also observed for V1 neurons both in the single unit recording studies in animal models [82, 61, 103, 104, 109, 116], and in human fMRI studies [124, 126, 140, 141], which suggest that such an effect in MT might be inherited from V1. However, a recent fMRI study showed that cortical activity in V1 shows a different pattern of surround modulation compared to hMT+, and the activity of MT but not V1 neurons agrees with the perceptual effect [99]. Furthermore, although some studies found surround suppression in V1, several other studies reported both suppression and facilitation depending on

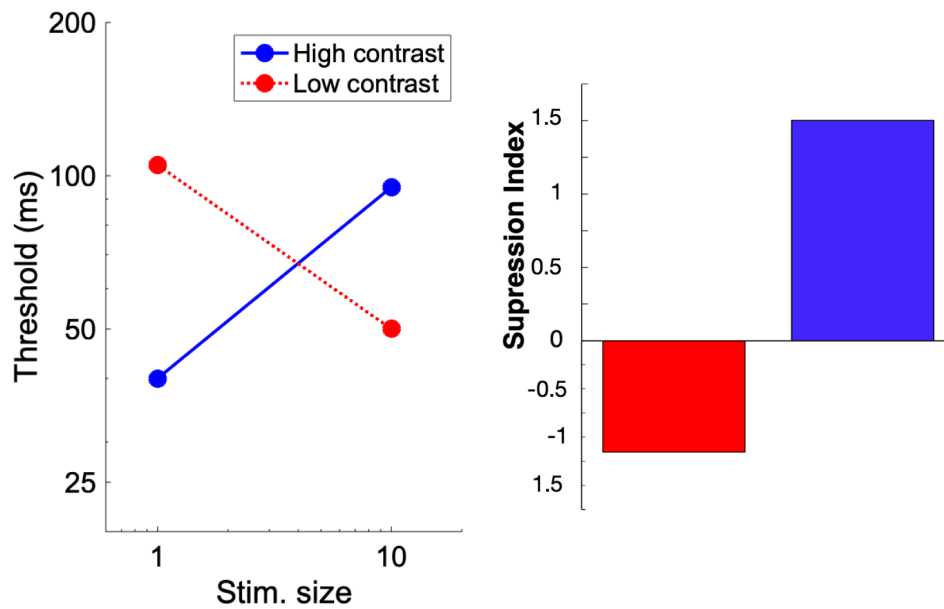


Figure 1.6: Typical effect of size-contrast interaction in motion perception. Left: Motion direction discrimination thresholds. As the size of a drifting grating increases, motion direction discrimination thresholds increase for high-contrast stimuli and decrease for low-contrast stimuli. Right: Suppression Index (SI) values. The suppression index quantifies the strength of the surround suppression. Higher positive SI values for high contrast indicate surround suppression, whereas negative SI values for low contrast indicate surround facilitation.

the presentation and attention conditions [123, 125]. Taken together, these findings support the idea that the perceptual consequences of surround suppression in human motion perception might arise from the MT area.

Surround suppression has different temporal characteristics. The fast early component is not selective for orientation, whereas the delayed late component is sharply tuned to orientation and elicits stronger suppression compared to the early component [65]. Different circuits and mechanisms may underlie different patterns of suppression. For example, in non-human primates, feedforward connections from LGN to Layer 4C yield spatially restricted and weaker surround suppression that is poorly tuned for orientation. On the other hand, horizontal connections in V1 and feedback connections from higher cortical areas (V2, V3/VLP, V5/MT) yield stronger surround suppression, spatially more extensive, and tuned for orientation. In line with this, Schallmo and colleagues [132] found two distinct neural mechanisms underlying the surround suppression in humans by examining the time course of the surround suppression using EEG. They found that the earliest visual component, C1, was suppressed by the surround gratings irrespective of orientation, which indicates the presence of a low-level mechanism that is not orientation-selective. They also found an N1 component observed later than C1, which was more strongly suppressed when the center and surround gratings were iso-oriented. Their results show that both the low-level mechanism that is untuned to orientation and appears early in time and the high-level mechanism that is orientation-selective and delayed in time contribute to the surround suppression.

More than being a low-level visual phenomenon, surround suppression is also frequently used to investigate multiple clinical conditions, including schizophrenia [100], major depressive disorder [142], autism spectrum disorder [102, 143, 144], Alzheimer’s disease [145], migraine [146], and epilepsy [147]. For example, abnormally weak surround suppression is observed in schizophrenia [100], major depressive disorder [142], and autism spectrum disorder (ASD) [98, 102, 143]. Importantly, weaker surround suppression was also observed with normal aging [148]. Although the reason underlying this abnormal surround suppression mechanism is still debated, the GABAergic system might provide an explanation for

this effect [100]. GABA is known to critically modulate lateral inhibitory interactions in the visual cortex, and GABAergic deficits have been reported in old age, schizophrenia, and depression [149, 150, 151]. It is hypothesized that an abnormal decrease in GABA concentration in the visual cortex might lead to decreased cortical inhibition, which, in turn, leads to weaker surround suppression. However, this hypothesis was not supported by more recent MR spectroscopy studies [97].

Other individual factors like gender and IQ have a significant effect on surround suppression. Previous studies revealed that there is a positive correlation between surround suppression and IQ [152]. There is also a gender difference in surround suppression such that males have shorter duration thresholds and weaker surround suppression compared to females [153].

1.3 Spatial Attention

We are constantly bombarded by numerous amounts of visual information coming from the environment, but for a given moment, only a tiny fraction of it can be processed effectively [154, 155]. Since we have limited processing capacity, a selection process must be made to allocate the limited computational resources to relevant visual input. Visual attention is one way to select the relevant signal and filter out others during visual processing.

Attention itself is a very elusive concept, as there are various forms of it [156]. For example, selective attention can be divided into top-down and bottom-up attention. While top-down attention is based on endogenous signals driven voluntarily, bottom-up attention is driven by exogenous signals like stimulus saliency. Another dichotomous form of attention is covert vs. overt attention. In overt attention, the visual selection process occurs with eye movements and motor behavior, whereas covert attention refers to attending to a certain stimulus and/or feature without moving the eyes. Finally, there is also object- and feature-based attention. Object-based attention refers to attending to a certain object that is

part of perceptual organization, and only features of that object benefit from the enhancing effects of attention. On the other hand, feature-based attention refers to selectively attending to a specific feature of objects throughout the visual field where only that feature benefits from the enhancing effects of attention. Importantly, these different forms of attention are not mutually exclusive, such that attention can operate endogenously without moving eyes (e.g., top-down covert attention).

The current thesis focuses on visual spatial attention, which is a form of visual attention characterized by directing attention toward a specific location in the visual field. In early studies, different metaphors were used to conceptualize spatial attention. For example, the “spotlight” attention metaphor emphasizes that any stimuli that fall within the attentional spotlight are selectively processed while the region outside the spotlight is processed less thoroughly or ignored [157]. A “zoom lens” metaphor, on the other hand, emphasizes variability in the size of the attentional field, the area that we selectively attend to for thorough processing [158]. To be more specific, attention acts as a zoom lens such that the focus of attention can be narrow and lead to more focused processing or can be wide and distributed in a larger area. Critically, due to limited processing capacity, processing efficacy decreases as the size of the attention field increases. However, these metaphors cannot fully characterize attentional processing, as growing evidence suggests that visual attention rather has gradient effects on sensory processing, such that enhanced visual processing at the attended location gradually decreases as the distance from the focus of attention increases [159, 160, 161]. In contrast, findings of other studies suggest that sensory processing around the focus of attention may be more complex than a simple gradient [162, 163, 164, 165, 166]. Specifically, a center-surround profile of attentional focus is observed in various experimental paradigms, including target detection, target discrimination, and item-matching tasks, where facilitated performance at the center of attentional focus (target location) gives its way to perceptual suppression in the vicinity of the target. In addition, the performance was better at the distractor locations far from the target than locations closer to the target [162, 163, 164, 167, 168]. These findings were later supported by human fMRI [169,

170, 171] as well as MEG studies [170, 172, 173, 174] where neural suppression is observed in the regions surrounding attended locations.

1.3.1 Spatial Attention and Changes in Visual Responses

Spatial attention shapes the response of neurons in the visual cortex. For example, when attention is directed to a single stimulus presented in the RF, faster, stronger, and less variable neural activation is observed compared to attention being directed away from the stimulus [175]. This effect of attention often resembles the overall change in the gain of neural response. However, this gain change seems rather multiplicative, such that the change in neural response is proportional to the initial response of the neuron. Importantly, when multiple stimuli are presented in or near RF, attention elicits more complex neural patterns, which cannot be explained by simple response gain. For example, when a neuron’s preferred and nonpreferred stimulus were presented simultaneously in the RF, directing attention to the nonpreferred stimulus elicited a decreased response, whereas attending to the preferred stimulus elicited an increased response [176, 177, 178, 179, 180, 181, 182]. On the other hand, if one of the preferred stimuli is presented in the RF center, and the other is presented in the RF surround, attending to the stimulus in the RF surround results in decreased neural activity [183].

Many theories and models have been proposed to explain these complex effects of attention. For example, Desimone and Duncan [156] proposed biased competition theory, which suggests that a group of neurons that encode multiple stimulus components compete, and attention biases this competition in favor of neurons that represent an attended stimulus or feature. Thus, attention introduces a top-down bias mainly driven by feedback signals arising from higher cortical areas, which lead to increased activation for the neurons that encode attended stimuli and suppressed activation for the unattended or irrelevant stimuli [156, 184]. Indeed, biased competition theory is supported by the findings of the single unit recordings in early visual areas [177, 178] as well as extrastriate areas

[176, 177, 185]. For example, as reported in the previous paragraph, attending to the nonpreferred stimulus presented simultaneously with the preferred stimulus in the RF elicits a decreased response, whereas attending to the preferred stimulus elicits an increased response, as neural competition is biased in favor of preferred stimuli [176].

Some of the previous findings show that the effects of attention on responses of neurons in the visual cortex resemble increasing contrast of the stimulus [178, 186, 187, 188]. Consistent with these neurophysiological findings, results of the psychophysics studies showed that attention indeed increased the perceived contrast of the stimulus [189, 190, 191, 192]. In line with this, the contrast gain hypothesis suggests that attention affects neural response in a way similar to multiplying the contrast of the unattended stimulus with a fixed value [156]. The contrast gain predicts that attention increases the firing rate of the neurons at intermediate contrast levels. On the other hand, since neural responses saturate at high contrast, attention has a small or no effect on the firing rate. Contrast gain is typically characterized as a leftward shift of the contrast-response function [3, 4] (see Figure 1.7). The neurophysiological and behavioral results suggest that attention indeed has larger effects on the stimuli presented at intermediate contrast compared to high contrast [187, 193]. The model also predicts that attending to a nonpreferred stimulus will increase its effective contrast, thereby making it more suppressive, which explains the finding that when nonpreferred and preferred stimuli are presented simultaneously in the RF, attending to the preferred stimulus results in an increased response, whereas attending to the nonpreferred stimulus leads to a decreased response [176].

On the contrary, as stated before, findings of the other studies suggest that attention modulates neural responses by multiplicatively scaling them with a response gain factor, with the largest effect of attention for the high contrast stimuli [179, 194]. Response gain is typically characterized as an upward shift of the contrast-response function [3, 4] (see Figure 1.7). In line with this, some single-unit recording studies showed that attention changes the overall gain of neural response in a multiplicative manner without altering the shape of neural tuning curves [185, 195]. Finally, there is evidence for the additive effect of

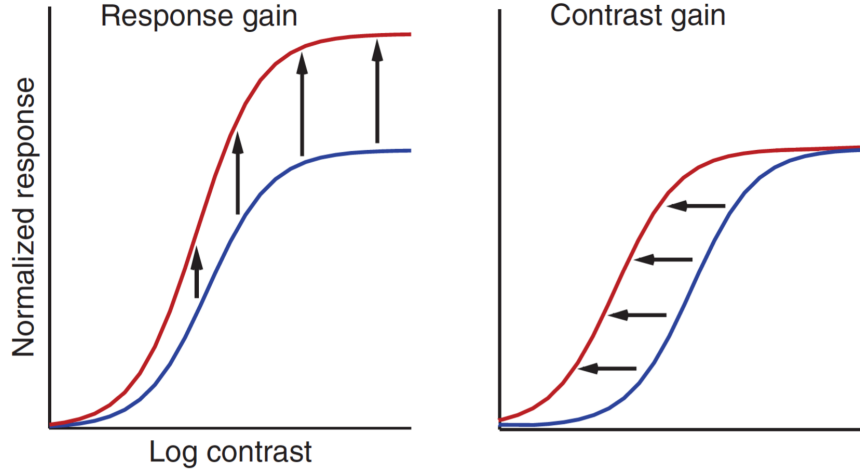


Figure 1.7: Illustration of contrast response functions for a stimulated neuron for response gain and contrast gain. Response gain is typically characterized as an upward shift of the contrast-response function, whereas contrast gain is typically characterized as a leftward shift of the contrast-response function [3, 4]

attention or changes between response gain and contrast gain [194].

Another influential framework to characterize visual attention is the feature-similarity gain principle, in which the level of attention-related gain modulation is based on the neuron’s selectivity for the attended feature [195, 196]. Specifically, the feature similarity gain model predicts that feature-based attention and spatial attention interact while determining an overall change in the gain of the neurons. The model can account for the observation that when a single stimulus is presented inside the RF or opposite hemifield with varied features such as orientation [185, 197], attending to either a preferred or a nonpreferred stimulus in the RF increases the neural activity by approximately the same factor.

Importantly, each of these various models and their predictions are combined into a single framework called the normalization model of attention (NMA), which incorporates spatial attention into the response normalization of the cortical neurons [4]. In other words, NMA can resolve previously discrepant results in the literature, predict all these different forms of attentional modulation and account for alternative theories of attention.

1.3.2 Normalization Model of Attention

1.3.2.1 Divisive Normalization Model

Normalization is often viewed as canonical computation in sensory systems, and it refers to the ratio between the response of a neuron and the summed activity of a pool of neighboring neurons [198, 199]. The neural summation in the visual cortex is not simply linear because of the antagonistic RF characteristics of the neurons. Therefore, divisive normalization is a more realistic framework to characterize the summation of the neural activity in the visual cortex.

Divisive normalization in sensory systems is characterized by the stimulus drive, which represents the excitatory response of neurons, and it is divided by the suppressive drive, which represents the summed activity of a pool of neurons. In the model, the inhibitory drive is spatially broader than the excitatory drive because it is pooled over a larger number of neurons. Excitatory and inhibitory drives together determine the overall firing rate of that neuron.

The model can be summarized by the following equation:

$$R(x, \theta, c) = \frac{E(x, \theta, c)}{S(x, \theta, c) + \sigma}, \quad (1.2)$$

where R is the predicted population response as a function of spatial position (x), direction of motion (θ), and contrast (c). E and S are the excitatory and suppressive drives, respectively, and σ is the semi-saturation constant, which prevents R from being undefined when S equals zero.

Recent studies suggest that the normalization model can explain many observations in the visual system [199], including neural summation, contrast saturation [200], cross-orientation suppression [201], and surround suppression [61]. Specifically, previous studies showed that using parameters derived from MT neurons in the normalization model can successfully predict surround suppression in motion perception both at the behavioral [97, 98] and neuronal levels [3, 97, 99, 202].

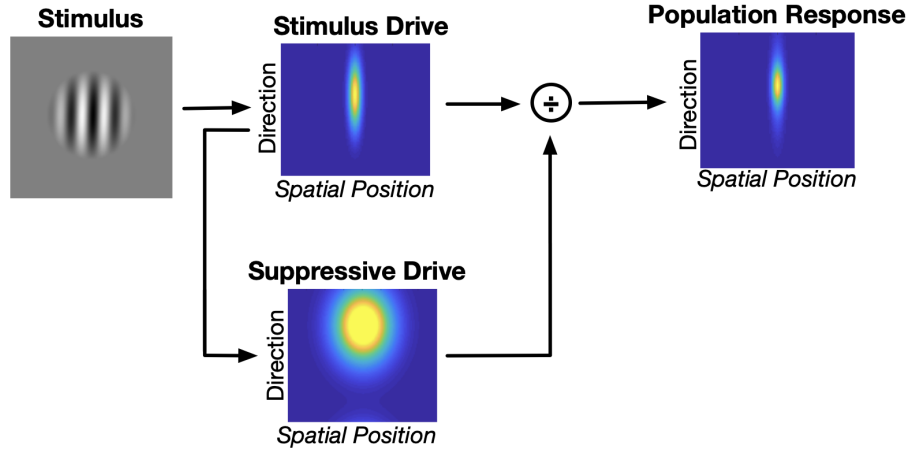


Figure 1.8: A schematic representation of the normalization model. The Excitatory Drive is normalized by the Suppressive Drive to determine population response (see Equation 1.2).

1.3.2.2 Normalization Model of Attention

Reynolds and Heeger [4] developed the normalization model of attention by incorporating the spatial extent of attention and response normalization. The model suggests that attention scales the excitatory and inhibitory drives received by a neuron, which together determine the overall firing rate of that neuron. Therefore, not only stimulus size but also the spatial and featural extent of the attention field contribute to response normalization in the visual cortex.

The model simulates the response of a population of neurons tuned to spatial position (spatial attention) and motion direction (feature-based attention). The model has three components:

1. Stimulus Drive, which represents the excitatory input a neuron receives;
2. Suppressive Drive, which represents the summed activity of a pool of neurons;
3. Attention Field, which modulates attentional gain for each neuron in the population according to spatial position and direction tuning (see Figure 1.9).

To determine the population response, the stimulus drive is multiplied by the attention field and then divided by the suppressive drive. The model can be summarized by the following equation:

$$R(x, \theta, c) = \frac{E(x, \theta, c) \times M(x, \theta, M_g)}{S(x, \theta, c) + \sigma}, \quad (1.3)$$

where R is the predicted population response as a function of spatial position (x), direction (θ), and contrast (c). E and S are the excitatory and suppressive drives, respectively. M represents the attention field, which reflects how spatial attention modulates the stimulus processing by scaling E , and M_g is the attentional gain factor that sets the spatial extent of the attention field M . σ is the semi-saturation constant, which prevents R from being undefined when S equals zero. The operator “ $\times$ ” represents element-wise multiplication (Hadamard product). Excitatory drive, E , is computed by

$$E(x, \theta, c) = e(x_e, \theta_e) * N(x, \theta, c), \quad (1.4)$$

where e is a two-dimensional (2-D) Gaussian function with the spatial position (x_e) and the direction (θ_e) that determines spatial and direction tuning, respectively, for the excitatory drive (E), $*$ denotes convolution and N is the neural representation of the stimulus, which is also a 2-dimensional Gaussian function with the stimulus position (x), and the direction (θ), and scaled by the contrast (c).

Suppressive drive, S , is computed by

$$S(x, \theta, c) = s(x_s, \theta_s) * \left(E(x, \theta, c) \times M(x, \theta, M_g) \right) \quad (1.5)$$

where s is another 2-D Gaussian function as e , but shows broader tuning in spatial position (x_s) and direction (θ_s). M represents the attention field, which reflects how spatial attention modulates the stimulus processing by scaling E . M is a 2-D Gaussian function whose spatial extent is set by the attentional gain factor M_g .

As it is stated earlier, while some results in the literature support the response gain [185, 195], other findings show a response pattern similar to contrast gain

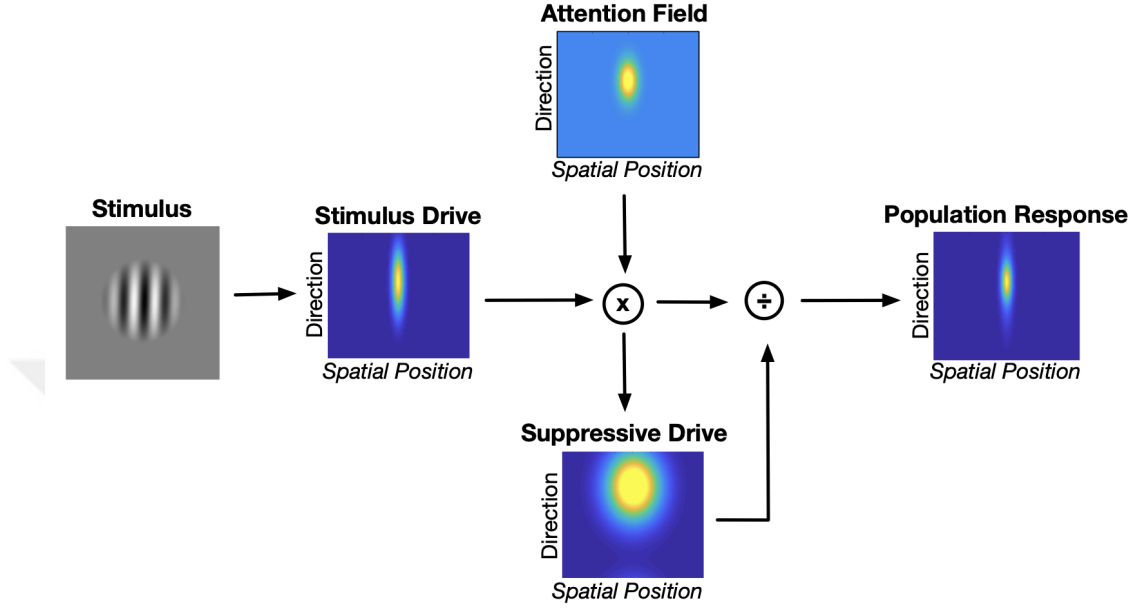


Figure 1.9: A schematic representation of the normalization model of attention. Stimulus Drive is multiplied by the attention field, then normalized by the Suppressive Drive to determine population response (see Equation 1.3).

[187, 193, 203]; or in between response and contrast gain [194], and the normalization model of attention can explain this complex pattern of results. The model suggests that attention scales the excitatory and inhibitory drives received by a neuron. Accordingly, the spatial spread of the attention field affects the contrast-response functions of neurons and, consequently, behavioral sensitivity. Specifically, the model suggests that attending to an area larger than the stimulus size results in contrast gain, whereas attending to an area smaller than the stimulus size results in response gain [4]. Although no single-unit-level study examined the plausibility of this prediction, results of human psychophysics experiments show that expected shifts in contrast-response function similar to contrast and response gain are observed depending on the spatial extent of attention [3, 204]. Therefore, attention does not always affect neural response in a manner similar to pure contrast gain or pure response gain. Rather, neurons can show both contrast gain and response gain, depending on the stimulus configuration and experimental design.

Furthermore, the normalization model can explain why shifting attention between preferred and nonpreferred stimuli, both presented in the RF, changes neural response drastically as it predicts an increase in effective contrast of the attended stimulus through the contrast gain mechanism [4, 205, 206, 207]. Importantly, the normalization model can also explain the simple response gain observed by attending to a single stimulus presented in RF [175]. NMA can also account for biased competition theory, as normalization is used in the early forms of theory to describe neural competition [178]. Besides, the model can explain feature-based attention as the featural extent of the attention field (i.e., the range of orientations attended) is also described in the model. Likewise, the model captures the predictions of the feature similarity model since neurons in the model are not only tuned to spatial position (spatial attention) but also to stimulus features (feature-based attention). To be more specific, the M_g parameter, attentional gain factor, modulates the gain of neurons based on attended location and/or feature [4, 205, 206, 207].

Importantly, NMA can also explain the interactions between attention and surround suppression [61, 104]. For example, the model predicts that a narrower attention field causes weaker suppression because it primarily increases the effect of the excitatory drive. Conversely, a wider attention field leads to stronger suppression because it increases both the effects of excitatory and inhibitory drives. The model also predicts that attending to the center of a stimulus should result in weaker neuronal suppression as the neural activity will be dominated by the center stimulus. On the other hand, directing attention to the surround stimulus should result in stronger suppression, as the neural activity will be dominated by the surround stimulus. Indeed, in non-human animals, directing attention to the center of a static stimulus results in weaker neuronal suppression compared to directing attention to the surround [131, 183, 186, 208].

1.4 Spatial Attention and Surround Suppression

Spatial attention has been known to modulate surround suppression both in humans [3, 123, 209, 122], and non-human animals [131, 175, 183, 186]. Specifically, in non-human animals, the effect of spatial attention on surround suppression is frequently demonstrated with single-unit recording studies using static stimuli. For example, Motter [210] presented multiple static stimuli in the visual field, one in the RF and others in the RF surround, and measured the single-unit activity of V1, V2, and V4 neurons in the macaque visual cortex. He found that when attention is directed to a stimulus presented in the RF center, neural activity increases, whereas when it is directed to stimuli in the RF surround, the neural response decreases. Similarly, Sundberg and colleagues [183] also showed that attention modulates center-surround interactions of the neurons in V4. To be more specific, they recorded the single unit activity while monkeys performed an attention-demanding multiple-object tracking task in which two static stimuli were presented together, one within the RF and the other in the RF surround. Consistent with the results of preceding studies, they found that attending to a stimulus in the RF reduces the suppressive effect of the stimuli presented in the RF surround. In other words, surround suppression was stronger when attention was directed to the surround than to the center. These results can be explained by the normalization model of attention as they are in line with the predictions of the model [4, 183, 186].

The effect of spatial attention using static stimuli, both behaviorally and neurally, is documented in humans, as well [3, 123, 209, 122]. For example, Freeman and colleagues [209] measured contrast detection thresholds while participants viewed the central target grating surrounded by flanker gratings. Specifically, they manipulated attention to the flankers and found that ignoring irrelevant pairs of flankers, similar to removing the flankers from the display, prevents the suppressive effect of flankers. Fievaris and Murray [122] provided more direct evidence that attention modulates center-surround interactions in humans. They

presented a central target along with two flanking gratings that have the same orientation and spatial frequency as the target or differ in one or both of these dimensions. They measured the contrast thresholds and found that a feature that was matched between the center and the flanker gratings makes the surrounding flankers more suppressive, thereby resulting in stronger suppression. Their results show that attention modulates surround suppression by facilitating the effect of the attended feature dimension. In line with this, in an fMRI study, Fiebert and Murray [123] also showed that a larger neural response in V1 is observed when attention is directed to the center grating compared to surround flanker gratings.

Dynamic stimuli, on the other hand, are used in only a few non-human animal studies to assess the effect of attention on surround suppression [211, 212]. Anton-Erxleben and colleagues [211], for example, demonstrated that spatial attention modulates center-surround interactions by changing the RF profile of the MT neurons in the macaque visual cortex. To be more specific, their results showed that attention shifts the RF center towards the attended location, such that attending to a moving stimulus presented inside the RF shrinks the RF, whereas shifting attention to the moving stimuli in the RF surround expands it. Their results also showed that the strength of the surround suppression increased for the attended location compared to the unattended location by increasing the influence of the attended stimulus on the neuron’s firing rate.

However, so far, there has been no direct study on humans to systematically examine the effect of the spatial extent of attention on surround suppression using motion stimuli. Because it is very challenging to examine the effect of endogenous attention on surround suppression with a visual paradigm that is based on prototypical visual stimulus. Indirectly, however, there is evidence that attention may modulate surround suppression with motion stimuli in humans. Using drifting gratings, autism spectrum disorder (ASD), patients have been found to exhibit weaker surround suppression compared to a neurotypical group [98]. The authors have argued that the weak suppression can be explained by a narrow spatial attention field and supported their argument with computer simulations using the divisive normalization model of attention [4].

On the other hand, the effect of the spatial extent of attention on neural activity in the visual cortex has been addressed in recent studies [204, 213]. Liu and colleagues [213] investigated how narrow vs. wide attention field modulates population receptive field (PRF) characteristics of neurons in the early visual cortex. They found that attending a narrower area in the focused attention condition leads to a smaller PRF with a higher amplitude compared to the distributed attention condition in V1. In addition, their results showed that attentional modulation was larger in the higher level area (i.e., V3) than in the lower areas (i.e., V1 and V2), which reflects the nature of the top-down feedback process of spatial attention. Moreover, Itthipuripat and colleagues [204] manipulated spatial scope of attention by varying possible locations of a small target disk (1.22° radius) and measured related activity using steady-state visual evoked potentials (SSVEP) in an EEG experiment. Specifically, in the focused attention condition, the target appeared within a 2.04° area, whereas in the distributed attention condition, it appeared in a 6.64° area. They found that signal-to-noise ratio (SNR) values were significantly higher in the focused attention condition compared to the distributed attention condition.

1.5 Current Study

Surround suppression is a very fundamental and common mechanism in biological vision since it is observed at many levels of the visual system [82, 61, 65, 73, 74, 75, 77, 83, 88, 89, 90] as well as other sensory modalities [68, 69, 70, 72], and it is a well-characterized phenomenon because it is based on a basic property of the neuron, namely antagonistic RF organization. Moreover, it contributes to many visual phenomena and functions such as figure-ground segregation [214, 215, 216], perceptual grouping [121, 134], perceptual inference [217], and efficient coding of information [218]. Therefore, it is an important tool for understanding visual information processing in humans.

Although surround suppression is initially considered a low-level mechanism

that arises from feedforward projections from the retina and horizontal connections within V1, there is also evidence that feedback projections from higher-level visual areas also contribute to this phenomenon [65]. The specific functional contributions of these feedback connections, however, remains unclear. Some studies have explored the effect of spatial attention on surround suppression with static stimuli [3, 123, 204, 209, 122], and a few non-human animal studies have used dynamic stimuli [211, 212]. Yet, no human study has systematically examined the effect of spatial extent of attention on surround suppression using motion stimuli. It is important to understand this effect as we are living in a dynamic environment, and using motion stimuli helps to better understand the nature of surround suppression in dynamic visual processes in the brain.

Critically, there is mounting evidence indicating that abnormal surround suppression is observed in many clinical disorders [98, 100, 102, 142, 143]. Therefore, it can also be used as a tool to understand the neural basis of abnormal visual processing and might shed light on the dynamics and shared origins of the clinical conditions, which may pave the way for developing new diagnosis and treatment methods. Moreover, investigating the effect of spatial attention on surround suppression can provide insights into the neural mechanisms underlying these processes and may have important implications for understanding the role of attention mechanisms in visual processing in both neurotypical and clinical populations.

Importantly, the effect of attention should be defined in neurotypicals first to be able to make comparisons with clinical populations and better understand the role of spatial attention in abnormal vision. However, as stated before, there has been no direct study to systematically examine the effect of the spatial extent of attention on surround suppression in human motion perception. In the current thesis, we sought to fill this gap in the literature and examine how the extent of spatial attention affects surround suppression in visual motion processing using psychophysics, functional magnetic resonance imaging (fMRI), and computational modeling.

For this purpose, we used a motion direction discrimination task to utilize a

well-studied effect in motion perception: as the size of a drifting grating increases, the observer’s ability to discriminate the motion direction of the grating increases if the stimulus is presented in low contrast and decreases if it is presented in high contrast. Further, we used a novel stimulus configuration that allows us to investigate the effect of endogenous attention with sinusoidal gratings, a frequently used prototypical visual stimulus, to examine surround suppression. Our stimulus consisted of a center grating surrounded by an annular grating. Center and surround gratings either drift in the same direction or in the opposite direction. Critically, we manipulated the spatial extent of attention in two attention conditions: narrow attention and wide attention. Participants were instructed to limit their attention to the central part of the stimulus under the narrow attention condition and to both the central and surround parts under the wide attention condition. This stimulus configuration and attentional manipulation allowed us to understand the role of spatial attention in center-surround interactions by using a simple but informative visual paradigm.

First, we conducted a behavioral experiment to investigate how perceptual correlates of surround suppression are modulated by the spatial extent of attention. To do so, we measured motion direction discrimination thresholds in humans using drifting gratings presented in different sizes and contrast levels. We expected to see higher duration thresholds for the wide attention condition compared to the narrow attention condition, indicating stronger surround suppression. The method and results of the behavioral experiment are introduced in Chapter 2.

Next, to understand the cortical mechanism that underlies the attentional modulation of surround suppression, we investigated how the BOLD fMRI response associated with surround suppression in hMT+ and V1 changes depending on the spatial extent of attention. For this purpose, we measured BOLD activity in hMT+ and V1, two possible regions where suppression is thought to arise, while the observers viewed drifting gratings and performed motion direction discrimination tasks, as in the behavioral experiment. We compared the magnitudes of BOLD responses between narrow attention and wide attention conditions within regions that correspond to the location and size of the center

grating. We expected to see a smaller BOLD response for the wide attention condition compared to the narrow attention condition, indicating stronger surround suppression. The method and results of the fMRI experiment are introduced in Chapter 3.

Next, we performed computer simulations using the divisive normalization model and incorporating the spatial extent of attention (i.e. normalization model of attention (NMA)[4]) to establish a link between the behavioral results and neuronal response characteristics. Finally, we simulated cortical responses in hMT+ and V1 to test the predictions of the model. In other words, we assessed whether the effect of attention on surround suppression described in this study could be explained by the NMA, as it has previously been done in the literature [3, 183, 186]. The method and results of the computational model are introduced in Chapter 4. In Chapter 5, we discuss the interpretations, implications, and potential applications of our results obtained from the psychophysics and fMRI experiments and model simulations.

Chapter 2

Behavioral Experiment

This chapter is based on the publication by Kiniklioglu, M., Boyaci, H. (2022). Increasing spatial extent of attention strengthens surround suppression. *Vision Research*, 199, 108074. <https://doi.org/10.1016/j.visres.2022.108074>. Reproduced (or reproduced in part) based on the author rights provided by Elsevier Publications.

Also, the studies and results presented in this chapter are presented in a preprint by Kiniklioglu, M., Boyaci, H. (2022). Increasing spatial extent of attention strengthens surround suppression, bioRxiv <https://doi.org/10.1101/2021.11.26.470072>

2.1 Introduction

This chapter is dedicated to the behavioral experiment of my thesis project, which aims to investigate how size-contrast interaction in motion perception is modulated by the spatial extent of attention at a perceptual level. Size-contrast interaction is well characterized both at a perceptual level and neuronal level. As the size of a drifting grating increases, direction discrimination thresholds increase for high contrast and decrease for low contrast stimuli [64]. In line

with the behavioral results, a neuron’s responses to a stimulus presented at the center of its receptive field are suppressed by iso-oriented stimuli presented in its surround [61, 62]. Single-unit recording studies in animal models showed that the spike rate of a neuron in V1 decreases when a stimulus is presented both within and outside of its classical receptive field, compared to when a stimulus falls only within its classical receptive field [61, 104, 82, 103, 116, 109]. Likewise, neural responses in humans measured by fMRI show a similar pattern of results: BOLD responses in V1 decrease when a central stimulus is presented with a surround compared to when it is presented alone [124, 125, 126].

Surround suppression is known to be critically affected by spatial attention [175]. For example, in non-human animals directing attention to the center of a static stimulus results in weaker neuronal suppression compared to directing attention to the surround [131, 183, 186, 208]. The effect of spatial attention using static stimuli, both behaviorally and neuronally, is documented in humans, as well [3, 123, 209, 122]. Dynamic stimuli, on the other hand, are used in only a few non-human animal studies to assess the effect of attention on surround suppression [211, 212]. No previous study on humans, to the best of our knowledge, has systematically examined the effect of attention on surround suppression using motion stimuli.

Here, we investigated the effect of the spatial extent of attention on surround suppression in humans using motion stimuli. We conducted a behavioral experiment with two attention conditions: narrow attention condition, in which participants were instructed to limit their attention to the center of the stimulus, and wide attention condition, in which they were instructed to attend to both the center and surround. If attention had an effect, based on the results in previous literature we would expect stronger suppression under the wide attention condition compared to the narrow attention condition.

2.2 Methods

2.2.1 Participants

Ten female volunteers (mean age= 26.7 years) participated in the experiment. All participants reported normal or corrected-to-normal vision and had no history of neurological or visual disorders. Participants gave their written informed consent before the experiment. The experimental protocols were approved by the Human Ethics Committee of Bilkent University.

2.2.2 Apparatus

Stimuli were generated using the Psychtoolbox (Brainard, 1997) with MATLAB 2018a (MathWorks, Natick, MA) and presented on a CRT monitor (HP P1230, 22 inches, 1280 x 1024 resolution, refresh rate 120 Hz). Participants were seated in a dark room with their heads stabilized using a chin rest at a distance of 75 cm from the monitor. A gray-scale look-up table was prepared through direct measurements of the luminance values (SpectroCAL, Cambridge Research Systems Ltd., UK) and used to ensure the presentation of correct luminance values. Responses were collected via a standard computer keyboard.

2.2.3 Stimuli and Design

Stimuli were vertically oriented drifting sinusoidal gratings (spatial frequency: 1 cycle per degree) weighted by two-dimensional raised cosine envelopes [102], the radius of which defined the stimulus size. Specifically, the stimulus consisted of a center grating surrounded by an annular grating (except the center-only configuration under the narrow attention condition, see below), which drifted within the stationary raised cosine envelopes (starting phase randomized) at a rate of $4^\circ/\text{s}$ either leftward or rightward (Figure 2.1). The stimuli were generated

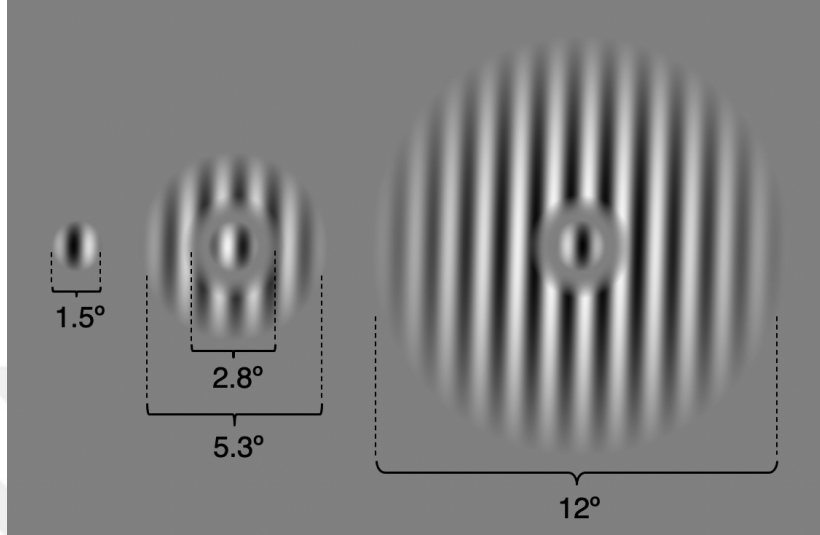


Figure 2.1: Center-only, small-surround, and large-surround configurations for high (98%) contrast stimuli.

using built-in functions of Psychtoolbox and presented foveally on a mid-gray background (16.09 cd/m^2).

In the narrow attention condition, a center sinusoidal grating is either presented alone or surrounded by a surround grating. Trials in which the center stimulus is presented alone (center-only) were used as a baseline to calculate the suppressive effect of the surround on the center. In the wide attention condition the center grating is always presented with a surround grating. The diameter of the center grating was 1.5° . The surround gratings were presented in two different sizes. In the small-surround configuration, the inner diameter of the surround was 2.8° , and its outer diameter was 5.3° . In the large-surround configuration, the inner diameter of the surround was 2.8° , and its outer diameter was 12° . The area between (1.5° to 2.8°) remained unstimulated to separate the center grating from the surround grating (Figure 2.1).

The motion directions of the center and surround gratings were randomly determined for each trial and were equally probable in either direction. In half of the trials, the center and surround gratings moved in the same direction, in the other half in opposite directions.

There were two contrast conditions in the experiment. The Michelson contrast of both center and surround gratings was 3% in the low contrast condition, and 98% in the high contrast condition. Two conditions of attention (narrow attention and wide attention), and two contrast levels (3% and 98%) were tested in separate sessions (4 experimental sessions in total) whereas two size levels (small-surround and large-surround) and two motion directions (same-direction and opposite-direction) were tested in the same session in randomized order on a trial-by-trial basis. The order of the sessions was counterbalanced for each participant and scheduled on different days.

For each trial, participants viewed foveally presented drifting gratings and performed a task about the perceived direction of motion via a key press. In the narrow attention condition, participants were asked to attend the center grating and report its motion direction. In the wide attention condition, participants were instructed to attend both the center and surround gratings: they first reported the drift direction of the center grating, then reported whether the center and surround gratings drifted in the same direction. This was done solely to encourage the participants to widen their attention fields. Hence, any difference in motion direction discrimination thresholds between narrow and wide attention conditions must reflect the effect of the spatial extent of attention as the stimulus presented in those conditions were identical (Figure 2.2).

In each trial duration of the presentation, defined as 2 standard deviations (SD) of a temporal Gaussian envelope [64, 219], was adjusted following an adaptive procedure (two interleaved 1-up 3-down staircases), based on the participants' judgments of the center grating drift direction in previous trials. Importantly, participants' judgments about the motion direction of the surround are not used for adaptively changing the stimulus duration; this second task is only used to encourage them to extend their attention field. There were two independently progressing staircases for each condition. One staircase started from a very short duration (25 ms), which made the task relatively harder, and the other started from a long duration (158 ms), which made the task relatively easier. There were 120 trials in each staircase. Each subject completed 1200 trials for narrow attention and 960 trials for wide attention conditions for each contrast. Each

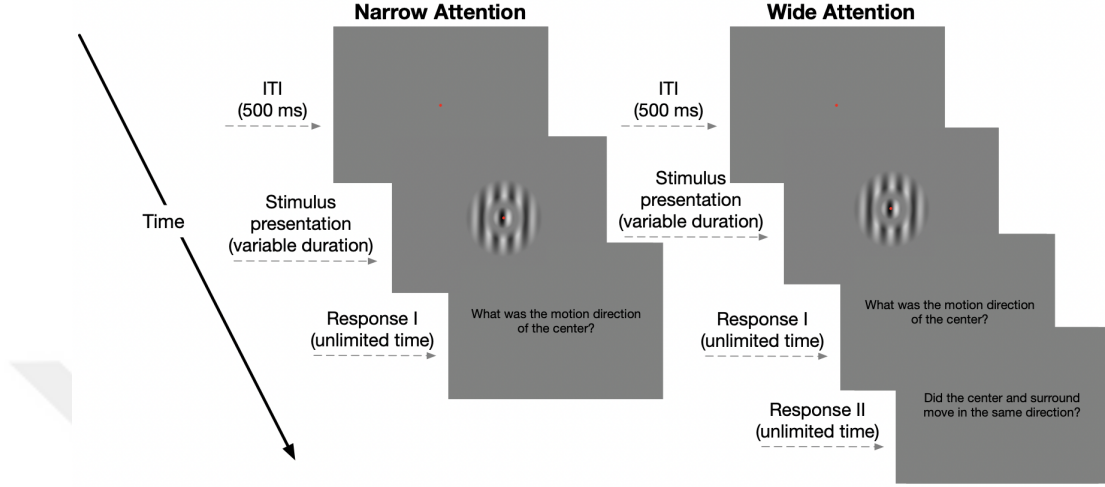


Figure 2.2: Experimental design for the narrow and wide attention conditions. Participants were asked to keep their eyes on a fixation point throughout the trial. Each trial began with a fixation point followed by the presentation of the stimulus, whose duration was adjusted with two interleaved 1-up 3-down staircases. In the narrow attention condition, participants reported the motion direction of the center grating. In the wide attention condition, participants first reported the drift direction of the central grating, then reported whether the central and annular gratings drifted in the same direction.

session took approximately 45 minutes. Brief break periods were given during the experiment.

2.2.4 Data Analysis

Duration thresholds (79% success rate) were calculated by fitting the responses with a Weibull function using the Palamedes toolbox [220] in MATLAB 2019a (MathWorks, Natick, MA) for each participant and condition. Next, using the threshold values, we calculated Suppression Indexes (SI) to quantify the strength of the surround suppression

$$SI_x = \frac{T_x - T_{1.5^\circ}}{T_{1.5^\circ}}, \quad x = 5.3^\circ, 12^\circ, \quad (2.1)$$

where T is the discrimination threshold for a given size. Higher positive values of SI indicate stronger surround suppression, whereas negative SI values mean surround facilitation. An SI of 0 means no suppression or facilitation.

We compared the SI values to “0” by applying a one-sample, two-tailed Student’s t-test with correction for multiple tests using SPSS Version 25 (SPSS Inc., Chicago, IL) to observe the expected effect of suppression. Next, we performed three-way repeated measures ANOVA on same-direction trials with three factors: attention (narrow- and wide-attention), size (small- and large-surround), and contrast (high- and low-contrast) to explore how the size-contrast interaction is affected by the spatial extent of the attention.

Then, we conducted pre-planned t-tests to test our research questions. Firstly, *is the surround suppression stronger in the wide attention condition compared to the narrow attention condition?* To find an answer to this question, we tested whether the mean *SI* under the wide attention condition is significantly larger than that under the narrow attention condition. Secondly, *does surround suppression increase with the size of the surround stimulus more strongly in the wide attention condition compared to the narrow attention condition?* To find an answer to this question, we tested whether the slope of the rise in *SI* with size is steeper under the wide attention condition compared to the narrow attention condition by using a two-tailed paired-samples t-test. Finally, *if there are these effects, are they purely because attention is allocated to a wider region, or is it because attention modulates surround suppression?* To answer this question and make sure that the observed effect is not a task-demand artifact, we performed two-tailed paired-samples Student’s t-test to test whether the effects of attention are stronger under the same-direction condition than the opposite-direction condition.

2.3 Results

Figure 2.3 shows motion direction discrimination thresholds averaged across all ten participants, and Figure 2.4 shows suppression indexes (*SI*, Methods) derived from the threshold values. Results of same direction trials (Figs. 2.3-2.4, A&B) exhibit a pattern that is consistent with literature [64], especially for the high contrast condition. Firstly, under both attention conditions, *SI* values increase

Table 2.1: Results of one-sample t -test for same-direction trials ($H_0 : SI = 0$). Numbers in degrees are the surround diameters.

	Mean Difference	df	t	p
Same Direction				
Narrow Low 5.3°	0.03	9	0.50	0.63
Narrow Low 12°	0.44	9	5.76	< 0.001*
Narrow High 5.3°	0.37	9	5.94	< 0.001*
Narrow High 12°	0.51	9	7.17	< 0.001*
Wide Low 5.3°	0.33	9	3.41	0.008
Wide Low 12°	1.15	9	5.94	< 0.001*
Wide High 5.3°	0.94	9	5.39	< 0.001*
Wide High 12°	1.13	9	6.16	< 0.001*

df = Degrees of Freedom, * indicates significance at $\alpha_{corr} = 0.00625$.

with size. Secondly, SI values are significantly larger than zero for all conditions except the low-contrast small-surround trials under both the narrow and wide attention conditions, which shows that for a low-contrast stimulus increase in size up to a value may lead to surround facilitation [97, 99, 64]. Table 2.1 shows one-sample t -test results for same direction trials.

More importantly, in all conditions, we visually observe stronger surround suppression under the wide compared to narrow attention condition (Figs. 2.3, 2.4). The robustness of this observation is supported by three-way repeated measures ANOVA results on same direction trials (Table 2.2), which showed significant main effects of attention and size, as well as size-contrast, attention-size, and attention-size-contrast interactions.

Next, we focus on our pre-planned comparisons. Our first comparison suggests that increasing the spatial extent of attention evokes stronger suppression: SI was significantly larger in the wide compared to the narrow attention condition (main effect of attention; $F_{(1,9)} = 35.97$, $p < 0.001$, $\eta^2 = 0.80$), and for all individual conditions, SI values were significantly higher in the wide attention condition compared to narrow attention condition ($ps < 0.002$, $\alpha_{corr}=0.0125$). Further, SI increased with the size of the surround more strongly in the wide compared to the narrow attention condition ($t_{(9)} = 3.64$, $p = 0.005$). These

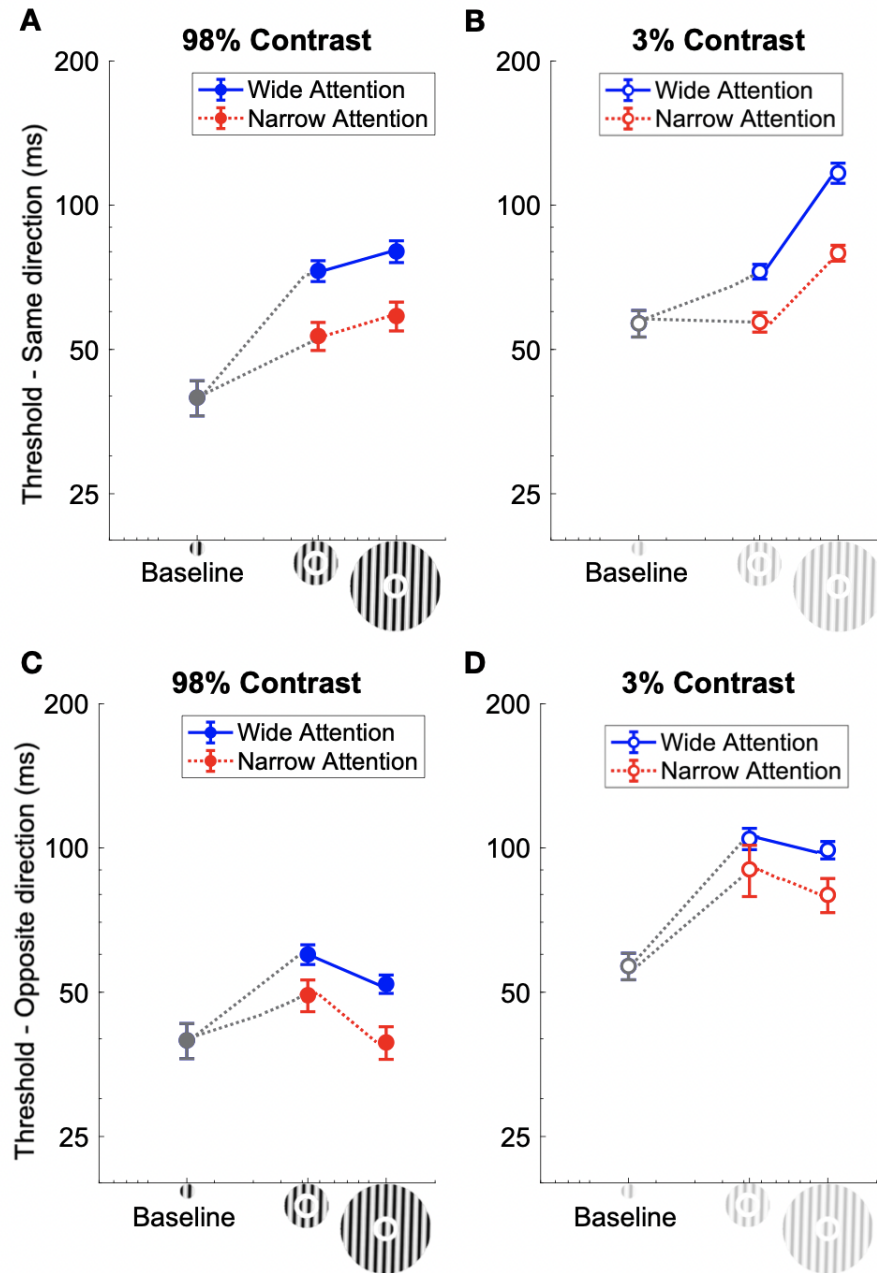


Figure 2.3: Behavioral results. Motion direction discrimination thresholds averaged across participants. A and B for same direction trials, C and D for opposite direction trials. Error bars represent SEM.

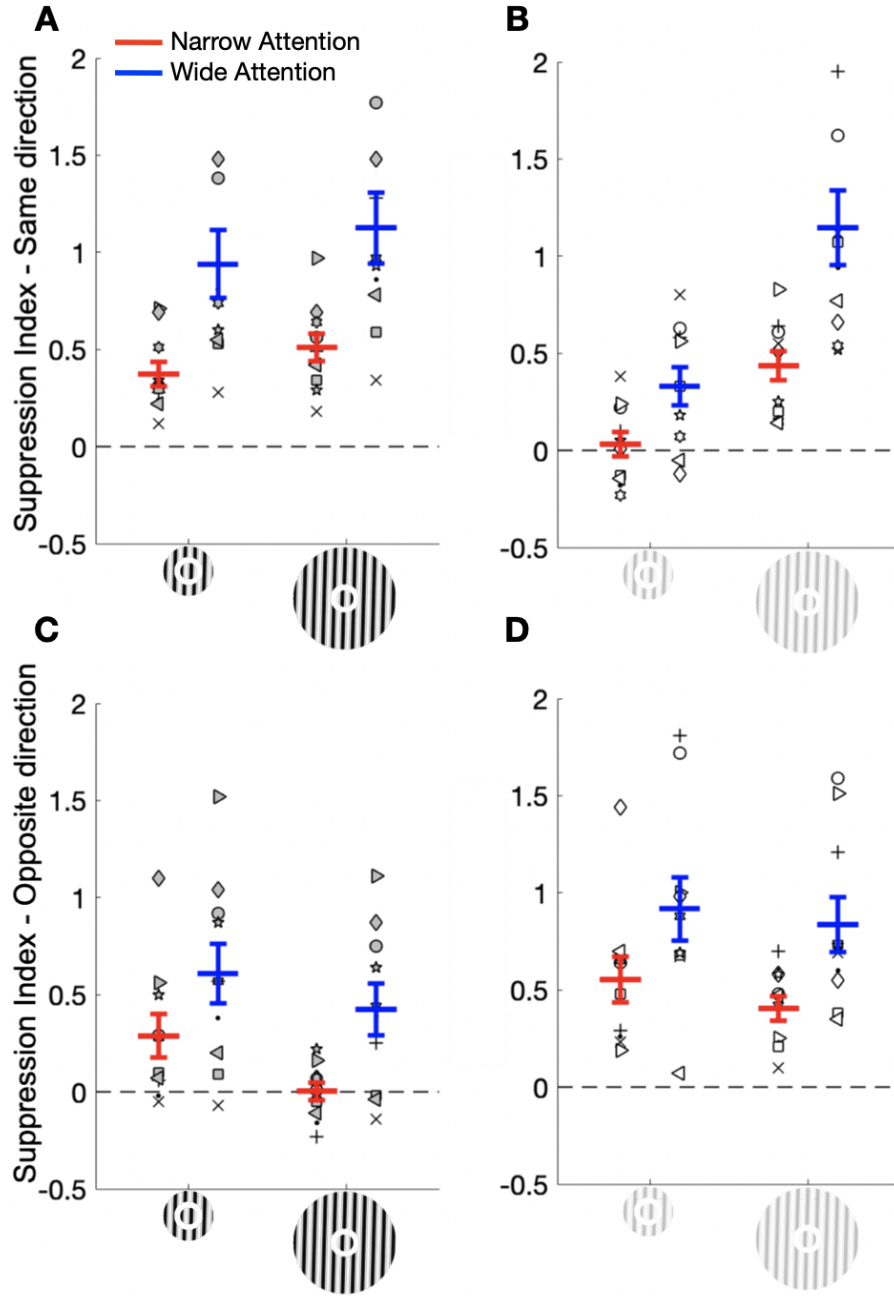


Figure 2.4: Suppression Indices (SI). A and B, same direction trials, C and D, opposite direction trials. Higher values of *SI* indicate stronger surround suppression, and negative *SI* values indicate surround facilitation. Symbols represent individual participants, and the red and blue lines show averages for narrow and wide attention conditions, respectively. Error bars represent SEM.

Table 2.2: Results of three-way ANOVA for same direction trials.

Source	SS	$F(1, 9)$	p	η^2
Same Direction				
Attention	6	35.97	<0.001	0.80
Contrast	1.25	4.75	0.057	0.35
Size	2.98	50.76	<0.001	0.85
Attention $\times$ Contrast	0.04	0.49	0.50	0.05
Attention $\times$ Size	0.26	13.22	0.005	0.60
Contrast $\times$ Size	1	31.32	<0.001	0.78
Attention $\times$ Contrast $\times$ Size	0.17	8.13	0.019	0.48

SS = Sum of Squares

provide answers to our first two research questions. Namely, they show that surround suppression is stronger in the wide attention condition compared to the narrow attention condition, and surround suppression increases with the size of the surround stimulus more strongly in the wide attention condition compared to the narrow attention condition.

It could be, however, argued that the results we found are just due to the demand of the second task (*i.e.*, a task-demand artifact), and they do not reflect the effects of surround suppression mechanisms per se. To control for this possible confound, we compared the results of same-direction and opposite-direction trials. We did this because it is well known that at the single-unit level surround suppression is reduced or eliminated when surround and center move in opposite directions [39, 104, 221, 222, 223]. Thus we reasoned that if our results reflect a true effect of attention on surround suppression, then the difference in SI between wide and narrow attention conditions should be smaller in the opposite direction trials compared to those in the same direction trials. Table 2.3 shows one-sample t -test results for opposite-direction trials. The patterns shown in Figure 2.4C and D for opposite-direction trials are clearly different than those in the same-direction trials shown in Figure 2.4A and B. To confirm, we applied two-tailed paired-samples Student's t -test to see whether the difference in SI values between the narrow and wide attention condition was significantly larger in the same-direction trials compared to opposite-direction trials. Results showed

Table 2.3: Results of one-sample t -test for opposite-direction trials ($H_0 : SI = 0$). Numbers in degrees are the surround diameters.

	Mean Difference	df	t	p
Opposite Direction				
Narrow Low 5.3°	0.56	9	4.74	< 0.001*
Narrow Low 12°	0.40	9	6.49	< 0.001*
Narrow High 5.3°	0.29	9	2.58	0.03
Narrow High 12°	0.004	9	0.09	0.93
Wide Low 5.3°	0.92	9	5.62	< 0.001*
Wide Low 12°	0.84	9	5.92	< 0.001*
Wide High 5.3°	0.61	9	3.97	0.003*
Wide High 12°	0.43	9	3.20	0.011

df = Degrees of Freedom, * indicates significance at $\alpha_{corr} = 0.00625$.

that the effect of attention (as quantified by the SI difference between narrow and wide attention conditions) was significantly stronger in the same-direction compared to the opposite-direction trials ($t_{(9)} = 3.11$, $p = 0.013$). These results suggest that attention had a weaker effect on the thresholds when the center and surround gratings drifted in opposite directions. This answers our third research question, namely that the effect found in same-direction trials is not an artifact of task demand. It reflects a genuine interaction between attention field and surround suppression.

Table 2.4 shows three-way repeated measures ANOVA results on opposite direction trials, which showed significant main effects of attention, size, as well as contrast.

Finally, we performed a post-hoc test on same direction trials to further explore whether attention interacts with size differently depending on the contrast of the stimulus in same-direction trials. For low contrast, the difference in SI values between narrow and wide attention conditions in small-surround configuration is significantly smaller than that in large-surround configuration ($t_{(9)} = 3.53$, $p = 0.006$; $\alpha_{corr} = 0.025$). However, for high contrast, the effect of attention was identical in different size conditions ($t_{(9)} = 0.96$, $p = 0.36$). This shows that the magnitude of the attention effect increases with the surround size in low contrast

Table 2.4: Results of three-way ANOVA for oopposite direction trials.

Source	SS	$F(1, 9)$	p	η^2
Opposite Direction				
Attention	2.95	10.24	0.011	0.53
Contrast	2.40	16.96	0.003	0.65
Size	0.62	10.57	0.010	0.54
Attention $\times$ Contrast	0.003	0.04	0.85	0.004
Attention $\times$ Size	0.04	0.87	0.38	0.09
Contrast $\times$ Size	0.07	2.40	0.16	0.21
Attention $\times$ Contrast $\times$ Size	0.001	0.05	0.83	0.005

SS = Sum of Squares

condition but does not change in high contrast condition.

2.4 Discussion

Here we investigated how the extent of spatial attention affects perceptual correlates of center-surround interaction in visual motion processing. Our results provide evidence that the spatial extent of attention affects size-contrast interaction in human motion perception. We found that increasing the spatial extent of attention evokes stronger suppression at a perceptual level. The magnitude of the attention effect increased with the size of the surround when the stimulus had low contrast but did not change when it had high contrast. Our results also showed that attention had a weaker effect when the center and surround gratings drifted in opposite directions.

Wider spatial attention leads to stronger surround suppression

We found that surround suppression was significantly stronger under the wide-attention condition compared to the narrow-attention condition. This is consistent with the findings of the single-unit studies in the literature. For example, Motter [210] presented multiple static stimuli in the visual field, one in the RF and

others in the RF surround, and found that when attention is directed to a stimulus presented in the RF center, neural activity in early visual cortex increases, whereas when it is directed to stimuli in the RF surround, the neural response decreases. Likewise, consistent with the preceding studies, Sundberg and colleagues [183] also found a similar effect of attention on center-surround interactions of the neurons in V4. They found that attending to a stimulus in the RF reduces the suppressive effect of the stimuli presented in the RF surround. These results indicate that surround suppression was weaker when attention was directed to the center than to the surround, paralleling our finding of lower thresholds (smaller suppression) in the narrow attention condition compared to the wide attention condition.

Critically, in previous studies, the modulatory effect of attention on surround suppression has been commonly demonstrated using a paradigm in which observers are asked to attend versus ignore a static stimulus [3, 123, 224, 225]. However, unlike in previous studies, here we investigated the effect of the spatial extent of attention rather than the mere presence or absence of spatial attention. Hence, to the best of our knowledge, our results are the first to systematically demonstrate that surround suppression in motion perception becomes stronger with a wider attention field.

Our results are partly in line with the studies that demonstrate the perceptual effect of attention on surround suppression [3, 209, 122]. For example, Flevaris and Murray [122] presented a central target along with two flanking gratings that have the same orientation and spatial frequency as the target or differ in one or both of these dimensions. They measured the contrast thresholds and found that attending to a feature that was matched between the center and the flanker gratings makes the surrounding flankers more suppressive, thereby resulting in stronger suppression. Their results show that attention modulates surround suppression by facilitating the effect of the attended feature dimension. Our behavioral findings showed that when the center and surround move in the same direction, attending to both center and surround results in a stronger suppression effect, parallel to their finding of increased suppression when the attended feature was matched between the central and flanking gratings.

Note that, even though there was a difference in the strength of surround suppression between the wide and narrow attention conditions for small-surround low-contrast stimuli, suppression indexes (SI) for those conditions did not reach significance ($p = 0.008$, marginally significant for wide attention condition at $\alpha_{corrected} = 0.00625$). This is not surprising, and it is consistent with previous studies reporting surround facilitation with low-contrast and relatively small stimuli [97, 99, 64]. Moreover, the pattern of our results, that is, the existence of surround suppression in high but not low contrast small stimuli, is also consistent with the response characteristics of neurons when a stimulus is presented in their non-classical receptive fields (RF) [82, 50].

Spatial attention interacts with size and contrast of the stimulus

We found that SI , on average, increases with size more strongly under the wide compared to the narrow attention condition. Assessing this effect further, we found that the difference in SI s between the narrow and wide attention conditions increases with size for low-contrast stimuli but does not change for high-contrast stimuli. This pattern of results may be partly related to the non-classical RF characteristics discussed in the previous paragraph.

It has been known that spatial attention affects contrast-response function and surround suppression at the perceptual level, but how it interacts with other contextual factors, such as size and contrast of the stimulus, was not systematically studied before in human motion perception. Our results here provide further knowledge to close this gap in the literature.

Spatial attention has a weaker effect when center and surround move in the opposite direction

We found that the attention effect (the difference in SI s under the wide and narrow attention conditions) was smaller when the center and surround drifted in opposite directions compared to when they drifted in the same direction. This shows that the effect of attention on surround suppression under the same-direction condition is not an artifact of the task demand. We reason as follows.

At the single-unit level, surround suppression is reduced or eliminated when surround and center move in opposite directions [39, 104, 221, 222, 223]. Thus, if the attention effect we find in the same direction trials is truly related to the surround suppression mechanisms, then it should be larger than that under the opposite direction condition. If the effect ensues as a result of the higher demand of the second task in the wide attention condition, however, then we would observe no difference between the same- and opposite-direction conditions. Our results show that the effect is stronger under the same-direction condition compared to different direction condition, and addresses this possible task-demand artifact confound.

There is limited information in the literature on the behavioral effects of surround suppression when center and surround move in opposite directions [138, 139, 226, 227, 228]. For example, Paffen and colleagues [228] found that large, high-contrast surround facilitated opposite-direction motion perception in the center, but this effect was not present for small- or low-contrast surrounds. This is partly consistent with our findings. Namely, we also found that for opposite-direction trials, suppression is more prominent in low-contrast trials, and it is reduced for high-contrast trials, especially for large-surround conditions. Tadin and colleagues [138] also reported facilitation from surround that moves in the opposite direction in a motion segregation task. Neurophysiological studies, on the other hand, have shown that attention affects the contrast-response functions when two different motion stimuli, one moving in the preferred one in the opposite direction, are presented simultaneously within the RF of a neuron [179, 193, 202]. To the best of our knowledge, however, our study is the first to demonstrate how attention affects surround suppression when center and surround drift in opposite directions.

Limitations

Under the limiting conditions of the pandemic, we were able to acquire data from only female participants in Chapter 2. [153] showed that males have lower motion discrimination thresholds than females. Yet, the pattern of results (e.g., increase in thresholds as the size of the high-contrast drifting grating increased)

did not change across the two sex groups. Therefore, we believe that all subjects being female does not affect the main aim of this study, which is to investigate how the spatial extent of attention modulates the motion discrimination thresholds with respect to size and contrast rather than the thresholds themselves.

Our results for the same direction trials in high contrast condition (Figure 2.3A) show a pattern that is consistent with literature [64]. But we did not find the often observed facilitation effect in the low contrast condition (Figure 2.3B). This might be due to the sizes and the spatial profile of our stimuli. The size of our center stimulus is larger than the ‘small’ patches commonly used in literature where facilitation is found. Further, we used raised cosine envelopes [102] rather than Gaussian envelopes used in many previous studies [64, 137]. A raised cosine envelope produces higher average contrast and a sharper edge profile than a Gaussian envelope. Indeed, careful scrutiny reveals that with sharper profiles and similar size of stimuli tested as in the current study, surround suppression is observed for low contrast patches in previous studies, as well [97, 98, 153]. Hence, the spatial profile and the size of the stimulus might affect the precise pattern of results in terms of suppression and facilitation observed in the current study. Nevertheless, this does not change the main conclusion of our findings, namely that the extent of spatial attention affects surround suppression. It would, however, certainly be very interesting to investigate in a future study how attention modulates surround facilitation by using a smaller center-only stimulus and/or a Gaussian spatial envelope.

Chapter 3

fMRI Experiment

3.1 Introduction

This chapter is dedicated to the fMRI experiment of my thesis project, which aims to investigate the neural correlates of the effect of spatial attention on surround suppression. As discussed in the earlier chapters, discriminating the motion direction of the drifting central grating becomes harder when presented with iso-oriented high contrast surround [96, 97, 99, 64, 229]. This perceptual effect has been explained by the surround suppression mechanism arising from antagonistic center-surround interactions of the neural populations in MT [64]. Indeed, previous psychophysics findings [64, 137] showed that larger motion duration thresholds were observed for conditions that evoked smaller MT activity [96, 97, 99, 101]. For example, firing rates of the MT neurons decrease for larger stimuli presented at high contrast [117]. Likewise, BOLD responses in MT decrease with increasing size for high contrast stimuli [96, 97]. Furthermore, disrupting hMT+ activity with TMS resulted in decreased surround suppression for high-contrast stimuli [101]. Although similar effects of surround suppression were also observed for V1 neurons both in the single unit recording studies in animal models [82, 61, 103, 104, 109, 116], and in human fMRI studies [124, 126, 140, 141]; a recent fMRI study showed that neural activity of hMT+ but not V1 neurons

agrees with the behavioral effect [99]. Taken together, these results suggest that the activity patterns of neurons in MT area is likely to be responsible for the perceptual effects of surround suppression in human motion perception.

Spatial attention has been known to modulate surround suppression both in humans [3, 123, 209, 122] and non-human animals [131, 175, 183, 186]. In line with this, as discussed in Chapter 2, we examined the effect of the spatial extent of attention on surround suppression in human motion perception using drifting gratings presented in different size and contrast levels in a psychophysics study [229]. We found that increasing spatial extent of attention causes stronger surround suppression, an observation that was also supported by predictions of the divisive normalization model [4]. Moreover, we showed that such an effect of attention is observed for both high and low contrast stimuli, and magnitude of this effect increases with the surround size in low contrast but does not change in high contrast [229]. However, so far, there has been no direct human neuroimaging study to examine the effect of the spatial extent of attention on surround suppression.

In the current study, we sought to investigate how the spatial extent of attention modulates surround suppression in V1 and hMT+ using fMRI. To address this, we first conducted a behavioral experiment to replicate our previous findings presented in Chapter 2 [229]. Then, we investigated how the BOLD fMRI response associated with surround suppression in hMT+ and V1 changes depending on the spatial extent of attention. For this purpose, we measured motion direction discrimination thresholds and associated neural activity in humans using high contrast drifting central gratings presented with large annular gratings in two attention conditions: a narrow attention condition in which participants were instructed to attend only to the center grating, and a wide attention condition in which they were asked to attend to both the center and surround. We hypothesized that if attention had an effect, we would observe smaller BOLD response (stronger surround suppression) under the wide attention condition compared to the narrow attention condition.

Critically, as the results of the behavioral experiment in Chapter 2 showed that

spatial attention affects both contrast levels similarly in large-surround trials, we decided to use only high contrast large-surround trials to reduce the number of conditions. This way, we were able to increase the number of trials per condition and get a better signal-to-noise ratio, which is limited in event-related fMRI experiment designs.

3.2 Methods

3.2.1 Participants

Ten volunteers (mean age = 25.7 years, eight female) participated in the experiment. All the volunteers who participated in the behavioral session also participated in the fMRI session. All participants reported normal or corrected-to-normal vision and had no history of neurological or visual disorders. Participants gave their written informed consent before the experiment. The experimental protocols were approved by the Human Ethics Committee of Bilkent University.

3.2.2 Psychophysics

3.2.2.1 Apparatus

The visual stimuli were presented on a mid-gray background (16.09 cd/m^2) using a CRT monitor (HP P1230, 22 inches, 1280 x 1024 resolution, 120 Hz refresh rate) in a dark room. Participants viewed the stimuli at a distance of 75 cm, with the head stabilized by a chin rest. Stimuli were programmed with the Psychophysics Toolbox (Brainard, 1997) on MATLAB 2018b (MathWorks, Natick, MA). A gray-scale look-up table was prepared through direct measurements of the luminance values (SpectroCAL, Cambridge Research Systems Ltd., UK) and used to ensure the presentation of correct luminance values.

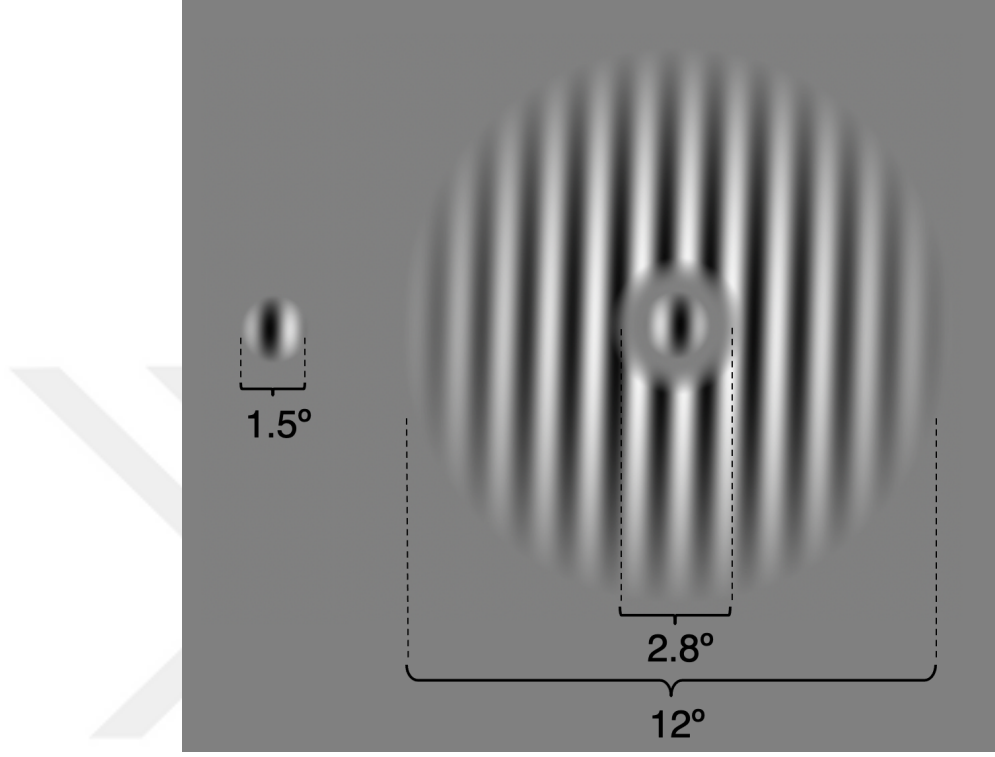


Figure 3.1: Center-only, and center+surround configurations.

3.2.2.2 Stimuli and Design

We used the same stimuli that were used in the behavioral experiment, described in Chapter 2. Briefly, we used drifting gratings (1 cycle/degree, $4^\circ/\text{s}$, starting phase randomized) weighted by two-dimensional raised cosine envelopes, the radius of which defined the stimulus size. The stimulus consisted of a center grating surrounded by an annular grating (except for the center-only configuration under the narrow attention condition, see below). The Michelson contrast of both center and surround gratings was 98%. The diameter of the center grating was 1.5° . The inner diameter of the surround grating was 2.8° , and its outer diameter was 12° . The area between (1.5° to 2.8°) remained unstimulated.

In the narrow attention condition, a center sinusoidal grating is either presented alone (center-only) or surrounded by a surround grating (center+surround). We used center-only trials as a baseline to calculate the suppressive effect of the surround on the center. In the wide attention condition, the

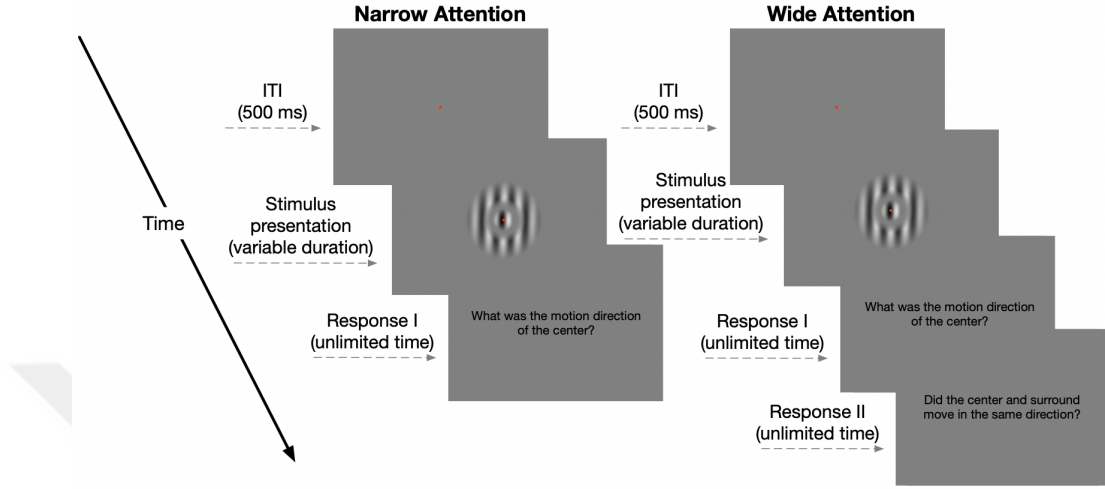


Figure 3.2: Trial sequence for the narrow and wide attention conditions in the behavioral tests conducted before fMRI scans. Participants were asked to fixate on the center of the display throughout the trial. Each trial began with a fixation point followed by the presentation of the stimulus, whose duration was adjusted with two interleaved 1-up, 3-down staircases. In the narrow attention condition, participants reported the motion direction of the center grating. In the wide attention condition, participants first reported the drift direction of the central grating, then reported whether the central and annular gratings drifted in the same direction.

center grating is always presented with a surround grating. The diameter of the center grating was 1.5° . The inner and the outer diameter of the surround were 2.8° and 12° , respectively. The area between (1.5° to 2.8°) remained unstimulated to separate the center grating from the surround grating (Figure 3.1).

The center and surround gratings either drifted in the same direction or in the opposite direction. For each trial, the motion directions of the center and surround gratings were determined randomly. In half of the trials, the center and surround gratings moved in the same direction; in the other half, they moved in opposite directions.

Two conditions of attention (narrow- and wide-attention) were tested in separate blocks, whereas two conditions of direction (same- and opposite-direction) were tested in the same block in a randomized order. The order of the blocks was counterbalanced for each participant and administered on the same day.

Throughout the experiment, participants viewed foveally presented drifting gratings and performed motion direction discrimination tasks via a standard keyboard press. In the narrow attention condition, participants were instructed to attend only to the center grating and report its motion direction. In the wide attention condition, participants were asked to attend both the center and surround gratings. They first reported the drift direction of the center grating, then reported whether the center and surround gratings drifted in the same direction (Figure 3.2). This second question was solely used to encourage the participants to extend their attention fields.

In each trial, the duration of the presentation, defined as two standard deviations (SD) of a temporal Gaussian envelope [64, 219], was adjusted with two interleaved 1-up, 3-down adaptive staircases, based on the participants' responses about the drift direction of the center grating in previous trials. There were two independently progressing staircases for each condition. One staircase started with a very short duration (33 ms) which made the task relatively harder, and the other started with a long duration (158 ms), which made the task relatively easier. There were 100 trials in each staircase. Each subject completed 600 trials for narrow attention and 400 trials for wide attention conditions. The experimental session took approximately 45 minutes. Brief break periods were given during the experiment.

3.2.2.3 Data Analysis

Duration thresholds (79% success rate) were estimated by fitting the responses with a Weibull function using the Palamedes toolbox [220] in MATLAB 2019a (MathWorks, Natick, MA) for each participant and condition. Next, using the threshold values, we calculated Suppression Indexes (SI) to quantify the strength of the surround suppression:

$$SI = \frac{T_{C+S} - T_C}{T_C}; \quad C = \text{center}, \quad C + S = \text{center} + \text{surround}, \quad (3.1)$$

where T is the discrimination threshold for a given stimulus condition. Higher positive values of SI indicate stronger surround suppression, whereas negative SI

values mean surround facilitation. An SI of 0 means no suppression or facilitation.

We compared the SI values to “0” by applying a one-sample, two-tailed Student’s t-test with correction for multiple tests using SPSS Version 25 (SPSS Inc., Chicago, IL) to assess the expected effect of suppression. Next, we performed a two-way repeated measures ANOVA with factors: attention (narrow- and wide-attention) and direction (same- and opposite-direction). Then, we conducted post-hoc tests to further explore how the spatial extent of attention affects surround suppression in different direction conditions.

3.2.3 fMRI

3.2.3.1 Image acquisition

fMRI data were collected on a 3 Tesla Siemens Trio MR scanner (Magnetom Trio, Siemens AG, Erlangen, Germany) with a 32-channel head coil in the National Magnetic Resonance Research Center (UMRAM), Bilkent University. Anatomical data were acquired using a T1-weighted 3-D anatomical scan (TR: 2600 ms, spatial resolution: 1 mm isotropic). Functional images were acquired with a T2*-weighted echo-planar imaging (EPI) sequence (TR: 2000 ms, TE: 35 ms, spatial resolution: 3x3x3 mm³). The stimuli were presented on a 32-inch (1360x768, 60 Hz) MR-compatible LED monitor (T-32, Troyka Med A.S., Ankara, Turkey). The monitor was placed near the rear end of the scanner bore and viewed by the participants from a distance of 156 cm via a mirror attached to the head coil. The stimuli were generated and presented using Matlab and Psychtoolbox. The session started with an anatomical scan, followed by three localizer runs and six functional runs, and took approximately 1 hour in total. During the scan, the participant’s response to the stimulus was collected via an MR-compatible fiber optic response box (Current Designs).

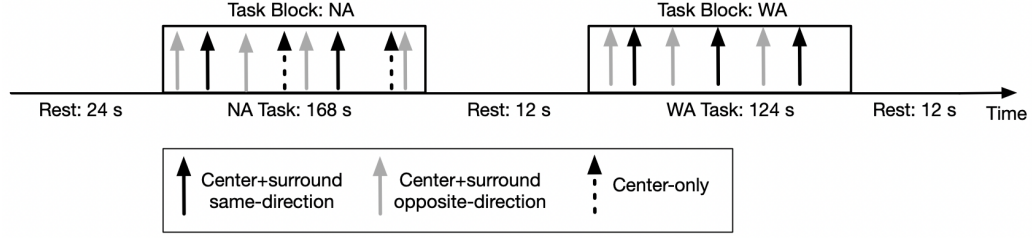


Figure 3.3: Schematic depiction of mixed blocked/event-related design of the fMRI experiment. In the paradigm, task blocks were alternated with rest blocks. The order of two block types (NA: narrow attention; WA: wide attention) was randomly determined. The narrow attention block consisted of center-only, same- and opposite-direction trials. Wide attention blocks consisted of same- and opposite-direction trials. Within each task block, trials were jittered with ITIs ranging from 4 to 8 s.

3.2.3.2 Stimuli and Design

The stimuli were drifting sinusoidal gratings as in the behavioral experiment (Figure 3.1). We used a mixed design in which narrow attention blocks were alternated with wide attention blocks. The experimental design is depicted in Figure 3.3. Two conditions of attention (narrow- and wide-attention) were tested in separate blocks, whereas two conditions of direction (same- and opposite-direction) were tested in the same block in a randomized order. Each run started with a 24 s fixation block (12 MR volumes; rest block) followed by a 168-s narrow attention block (task block; 84 MR volumes) or a 124-s wide attention block (task block; 62 MR volumes) followed by 12 s of fixation (6 MR volumes; rest block), a 168-s narrow attention block (task block; 84 MR volumes) or a 124-s wide attention block (task block; 62 MR volumes), and 12 s of fixation (6 MR volumes; rest block). The order of the blocks was randomized in a run. Within the task blocks, the intertrial interval (ITI) was jittered between 4 s and 8 s. Within a task block, each condition (three conditions for narrow attention and two conditions for wide attention) was presented six times. The total duration of a functional run was around 5 minutes. There were six experimental runs in the session.

Stimuli were presented for 150 ms on a mid-gray background. As in the behavioral experiment, the participants viewed foveally presented drifting gratings

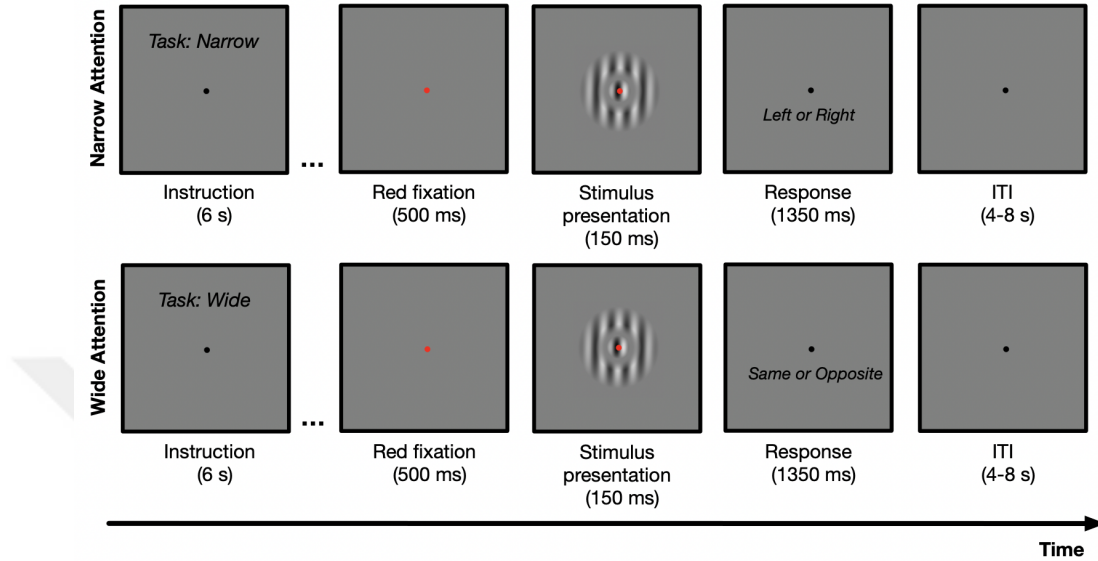


Figure 3.4: Trial sequence of the narrow- and wide-attention blocks in the functional run. Participants were asked to fixate on the center of the display throughout the trial. At the beginning of the each block, instruction for the task was written on the instruction screen in detail. In the narrow attention block, the participants were instructed to attend only to the center grating and report its motion direction. In the wide attention block, the participants were instructed to attend both center and surround gratings and report whether the central and annular gratings drifted in the same direction. Each trial began with a fixation point, followed by the presentation of the stimulus for 150 ms. In the real experiment, the possible answers were not written on response screen.

and reported the perceived direction of motion via an MR-compatible response box. In the narrow attention condition, participants were asked to attend to the center grating and report its motion direction. In the wide attention condition, the participants were instructed to attend both to the center and surround gratings. However, they only reported whether the center and surround gratings drifted in the same direction (see Figure 3.4). Critically, unlike the behavioral experiment, we only ask one question to identify the neural activity associated with the smaller vs. larger spatial attention width since asking two consecutive questions would elicit different neural activity.

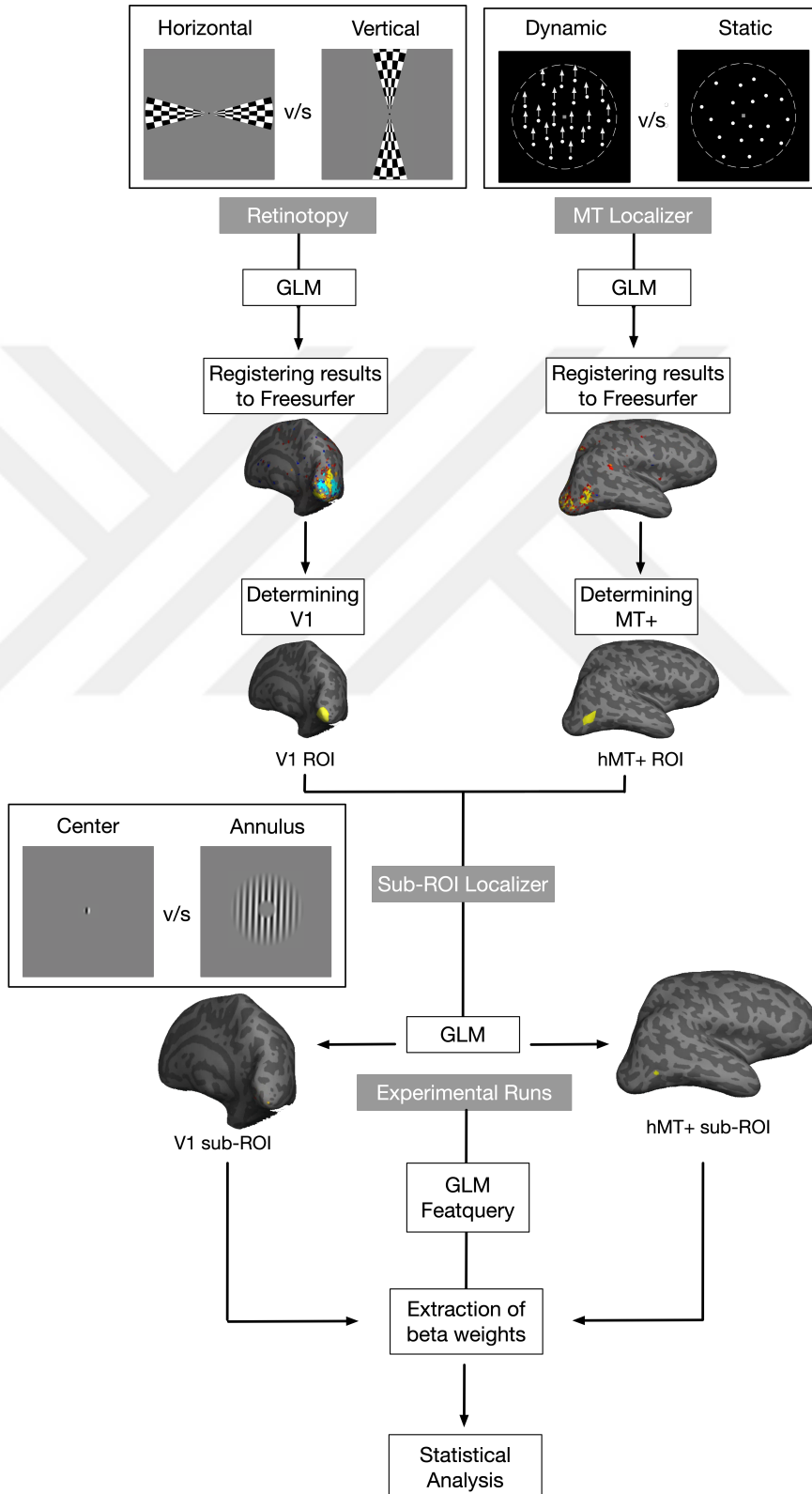


Figure 3.5: Analysis pipeline.

3.2.3.3 hMT+ and V1 Identification

We identified the hMT+ area using standard methods in the literature [230]. Specifically, we used a field of moving and static dots (Figure 3.5). The dot field consisted of 100 randomly positioned white dots presented foveally within a 12-degree diameter circular aperture on a black background. The dots moved in three different trajectories: cardinal (left-right; up-down), angular (clockwise-counterclockwise), and radial (expanding - contracting). The direction of motion is altered every 2 s to prevent adaptation. The localizer runs started with a 24 s blank period, followed by 12 s blocks of a field of static dots alternating with 12 s blocks of a field of dynamic dots. There were six blocks of dynamic and static field presentations in a run. Throughout the entire run, the participant was required to maintain central fixation and perform a demanding fixation task in which they were asked to detect changes in the color of the fixation point. We performed GLM to differentiate the BOLD responses during the presentation of dynamic and static stimuli. Voxels that respond more strongly to dynamic compared to static stimuli at the ascending tip of the inferior temporal sulcus were identified as hMT+.

We identified each participant’s V1 in a separate run. Similar to established retinotopic mapping methods in the literature [231, 232], we used flickering checkerboard-patterned wedges (Figure 3.5). However, as we only interested in V1/V2 boundry, instead of rotating and expanding wedges, we used alternating horizontal and vertical wedge stimuli in this localizer [233, 234]. Nonetheless, this protocol and standard retinotopic mapping method used in literature are both based on same idea that vertical meridian give us V1/V2 boundry. During this localizer run, 16-s horizontal checkerboard stimuli were alternated with 16 s vertical checkerboard stimuli. This cycle repeated eight times in a run. Throughout the entire run, the participant was required to maintain central fixation and perform a demanding fixation task in which they were asked to detect changes in the color of the fixation point. We used a general linear model (GLM) to differentiate the BOLD responses during the presentation of horizontal and vertical wedge stimuli. Voxels that respond more strongly to horizontal compared

to vertical wedge stimuli provide us with the V1-V2 boundary. The voxels that fell in or around the calcarine sulcus and between the dorsal and ventral V1-V2 boundaries were identified as V1.

3.2.3.4 hMT+ and V1 sub-ROI Localization

We identified sub-ROI within hMT+ and V1 using an independent localizer run (Figure 3.5). In this localizer, we sought to localize the hMT+ and V1 voxels corresponding to the spatial location and size of the center grating while the participants were viewing drifting high contrast (98%) gratings whose size and location were exactly the same as in the behavioral experiment and the functional runs (see Figure 3.1). Specifically, center-only gratings and annular gratings were presented in different blocks. This localizer run consisted of 12 s of active blocks alternated with 12 s rest blocks, and this cycle was repeated six times in the run. Throughout the entire run, the participant was required to maintain central fixation and perform a demanding fixation task in which they were asked to detect changes in the color of the fixation point. We applied GLM to differentiate the BOLD responses during the presentation of center and annular gratings. V1 and hMT+ voxels that respond more strongly to the center grating compared to the annular grating were identified as the V1 and hMT+ sub-ROI, respectively. All subsequent analyses were performed using the data extracted from these sub-ROIs.

3.2.4 Data Analysis

3.2.4.1 Preprocessing

The high-resolution anatomical images are skull stripped, segmented to white and gray matter, normalized for intensity, smoothed, and surface reconstructed by using FreeSurfer’s *recon-all* command [235, 236].



Figure 3.6: Location of the representative hMT+ and V1 ROIs on the inflated surface.

The localizer and functional runs were preprocessed using the FMRIB Software Library (FSL) package (www.fmrib.ox.ac.uk/fsl) and FEAT version 6.0. and included motion correction with MCFLIRT, high-pass temporal filtering (100 s), and skull stripping of structural images with BET and registration with. FMRI data were registered to the subject’s high-resolution anatomical images and the standard Montreal Neurological Institute (MNI) 2-mm brain using FLIRT.

3.2.4.2 Region of interest construction

The hMT+ area was identified by applying GLM using FSL’s FEAT program. For removing the temporal autocorrelations, FILM prewhitening was applied [237]. For thresholding data, the $P = 0.05$ (corrected) threshold was set as the cut point. Voxels that respond more strongly to dynamic compared to static stimuli were identified using GLM. Next, we registered these FSL’s FEAT results to Freesurfer and overlaid the statistical map on the surface using *tksurfer* command. Then we loaded the MT label from FreeSurfer’s anatomical delineation for guidance. Voxels at the ascending tip of the inferior temporal sulcus were identified as hMT+ for the participant and used it as a mask for the hMT+ sub-ROI localization (see Figure 3.5).

The V1 area was identified by applying GLM using FSL’s FMRI Expert Analysis Tool (FEAT). For removing the temporal autocorrelations, FILM prewhitening was applied [237]. Voxels that respond more strongly to horizontal compared to vertical wedge stimuli provided us with the V1-V2 boundaries. Next, we registered these FSL’s FEAT results to Freesurfer and overlaid the statistical map on the surface using the *tksurfer* program. Then, we loaded the V1 label from FreeSurfer’s anatomical delineation for guidance and drew V1-V2 boundaries. The voxels that fell in or around the calcarine sulcus were identified as V1 for the participant and used as a mask for the V1 sub-ROI localization (Figure 3.6).

To find V1 and hMT+ sub-ROIs, we analyzed the independent localizer run by applying GLM using FSL’s FEAT. We identified voxels that respond more strongly to the center compared to the annular grating. For removing the temporal autocorrelations, FILM prewhitening was applied [237]. The V1 and hMT+ labels mentioned above were used as a pre-threshold mask, such that only the voxels that stayed within the masks were included in the analysis. The activated regions were used as hMT+ and V1 masks, respectively, for the analysis of the functional runs.

3.2.4.3 Activation within regions of interests

Functional data were analyzed using FSL [238, 239]. As a first-level, we conducted event-related voxelwise analyses and modeled the BOLD response elicited by each trial by convolving each condition’s regressors with a double-gamma hemodynamic response function (HRF). Nuisance regressors for linear motion (derived from MCFLIRT) were also included in the model. For removing the temporal autocorrelations, FILM prewhitening was applied [237]. Contrasts were calculated, focusing on the main effect of each condition. The second level of the functional analysis involved a fixed-effects combination of all six runs for each participant, providing a participant-by-participant average of the first level contrasts.

Then, to estimate the magnitude of activation within the sub-ROIs, we extracted parameter estimates for each condition using the Featquery tool (FMRIB, Oxford). Specifically, we used V1 and hMT+ sub-ROI masks that were created for each participant (see Region of Interest Construction) to extract beta values for each trial type across all voxels within each of the predefined ROIs (see Figure 3.5).

Next, to quantify the changes in fMRI response evoked by increasing surround size and also to draw a link between behavioral and fMRI results, we calculated a Suppression Index (SI) defined as

$$SI = B_C - B_{C+S}; \quad C = \text{center}, \quad C + S = \text{center} + \text{surround}, \quad (3.2)$$

where B is the beta value for the given condition. A negative SI means increased response with surround (surround facilitation), and a positive SI means decreased response with surround (surround suppression). An SI of 0 represents no suppression.

First, we compared the SI values to “0” by applying a one-sample, two-tailed Student’s t-test with correction for multiple tests using SPSS Version 25 (SPSS Inc., Chicago, IL) to observe the expected effect of suppression. Next, we performed a two-way ANOVA on the SIs with two factors: attention (narrow attention and wide attention) and direction (same-direction and opposite-direction) for each ROI. Then, we conduct a post-hoc test to further explore how attention affects surround suppression for different direction conditions (see Figure 3.5).

3.3 Results

3.3.1 Behavioral Results

Figure 3.7 shows motion direction discrimination thresholds averaged across all ten participants and suppression indexes (*SI*) derived from the threshold values. Firstly, under both attention conditions, thresholds increase with size for the

same-direction trials. Secondly, SI values are significantly larger than zero for both attention conditions in same direction trials ($ps < 0.001$), but not in opposite direction trials ($ps > 0.05$).

More importantly, in the same direction trials, we visually observe stronger surround suppression under the wide compared to narrow attention condition (Figure 3.7). The robustness of this observation is supported by two-way repeated measures ANOVA results, which showed significant main effects of attention ($F(1,9) = 232.78$, $p < 0.001$) and direction ($F(1,9) = 226.76$, $p < 0.001$), as well as attention-direction interaction ($F(1,9) = 251.30$, $p < 0.001$).

Next, we focused on the post-hoc tests to further examine how the effect of attention on surround suppression changes depending on the motion direction. Paired-sample t -test results showed that SI values are significantly larger in the wide attention condition compared to the narrow attention condition only in same-direction trials ($t(9) = -2.75$, $p = 0.022$; $a_{corr} = 0.025$), not in opposite direction trials ($t(9) = -0.24$, $p > 0.05$). Hence, these results successfully replicate our previous behavioral results [229] such that surround suppression was significantly stronger under the wide attention condition for the same direction trials.

3.3.2 fMRI Results

3.3.2.1 hMT+

Figure 3.8 shows fMRI BOLD responses extracted from hMT+ sub-ROI averaged across all ten participants and suppression indexes (SI) derived from them. Firstly, we note that under both attention conditions, the BOLD response decreases with size for the same direction trials. Secondly, SI values are significantly larger than zero for both attention conditions in same-direction trials ($ps < 0.0125$), not in opposite-direction trials ($ps > 0.05$).

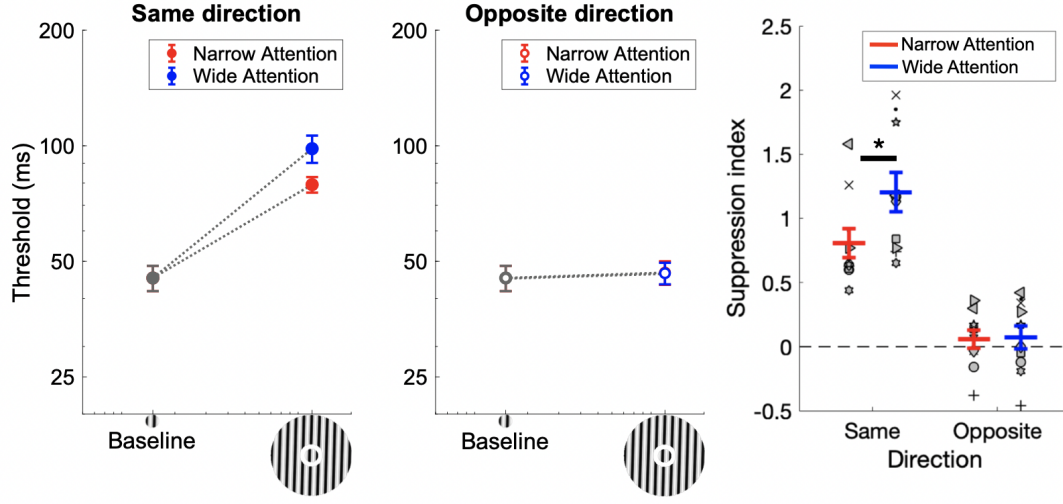


Figure 3.7: Behavioral results. Left: Motion direction discrimination thresholds averaged across participants. Right: Suppression Indices (SI). Higher values of SI indicate stronger surround suppression and negative SI values indicate surround facilitation. Symbols represent individual participants, and the red and blue lines show averages for narrow and wide attention conditions, respectively. * indicates significance at $p < 0.05$. Error bars represent SEM.

More importantly, in the same direction trials, we visually and statistically observe stronger surround suppression under the wide compared to narrow attention condition (Figure 3.8). Furthermore, two-way repeated measures ANOVA results revealed that there was no main effect of attention ($F(1,9) = 1.05$, $p > 0.05$, $\eta^2 = 0.10$), but there was a significant main effect of direction ($F(1,9) = 19.89$, $p < 0.05$, $\eta^2 = 0.69$), as well as an interaction between attention and direction ($F(1,9) = 32.81$, $p < 0.001$, $\eta^2 = 0.79$).

Finally, we performed a post-hoc test to further explore how attention affects surround suppression under different direction conditions. Paired-sample test results showed that SI values significantly larger in the wide attention condition compared to the narrow attention condition only in same-direction trials ($t(9) = 2.90$, $p = 0.018$; $a_{corr} = 0.025$). For the opposite direction of motion, there was no significant difference in activity between narrow and wide attention conditions ($t(9) = -1.18$, $p > 0.05$). In line with behavioral results, these results suggest that increasing the spatial extent of attention causes stronger neural suppression in hMT+ in the same direction trials.

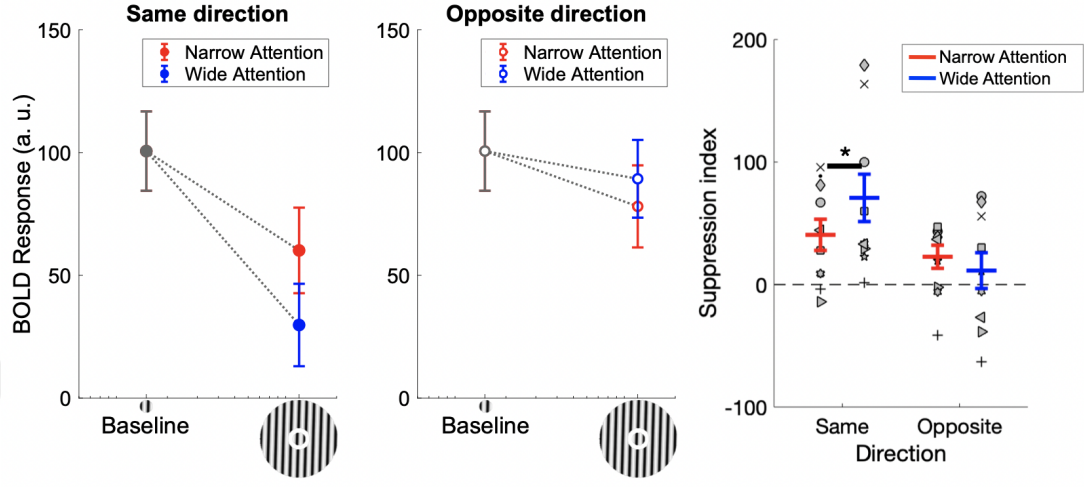


Figure 3.8: hMT+ results. Left: Beta values extracted from averaged across participants. Right: Suppression Indices (SI) derived from beta values. Red and blue lines indicate narrow and wide attention conditions, respectively. * indicates significance at $p < 0.05$. Error bars represent SEM.

3.3.2.2 V1

Figure 3.9 shows fMRI BOLD responses extracted from the V1 sub-ROIs averaged across all ten participants and the suppression indexes (SI) derived from them. Firstly, we note that under the wide attention condition, the BOLD response decreased with size for same-direction trials. Increasing the size of the stimuli, however, resulted in no change in the BOLD response for the narrow attention condition. In line with that, SI values are significantly larger than zero only for wide attention same-direction trials ($p < 0.01$; $a_{corr} = 0.0125$). For the opposite direction trials and same-direction narrow attention trials, SI values do not significantly differ from zero ($ps > 0.05$).

More importantly, two-way repeated-measures ANOVA results showed a marginally significant effect of direction ($F(1,9) = 4.92$, $p < 0.054$, $\eta^2 = 0.35$). However, neither the main effect of attention nor the attention-direction interaction reached significance ($ps > 0.05$).

Finally, although neural suppression in V1 for same-direction trials increased as the spatial extent of attention increased, it was only marginally significant. The

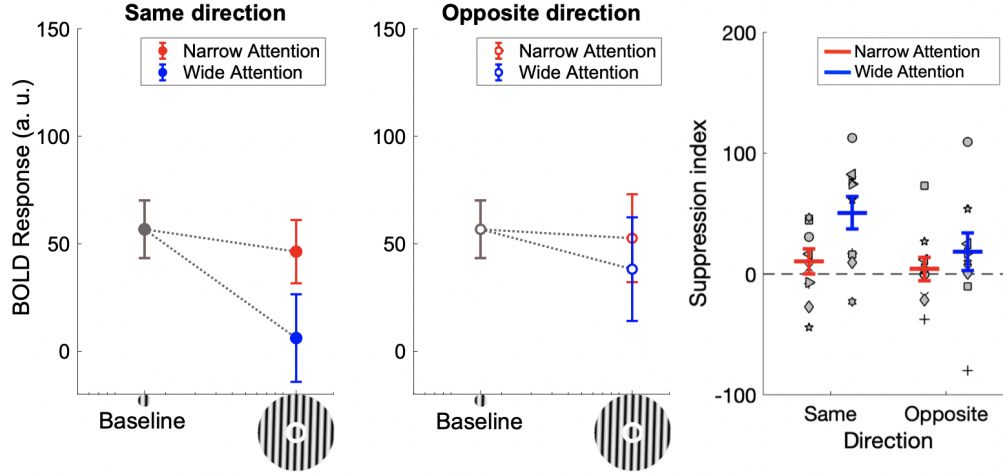


Figure 3.9: V1 results. Left: Beta values extracted from averaged across participants. Right: Suppression Indices (SI) derived from beta values. Red and blue lines indicate narrow and wide attention conditions, respectively. Error bars represent SEM.

paired-sample test results showed that SI values marginally larger in the wide attention condition compared to the narrow attention condition only in same-direction trials ($t(9) = 2.34$, $p = 0.044$; $a_{corr} = 0.025$). However, for the opposite direction of motion, there was no significant difference in activity between narrow and wide attention conditions ($t(9) = 0.88$, $p > 0.05$).

3.3.3 Comparing Behavioral and fMRI Results

To draw a link between the behavioral and fMRI results, we calculated a sensitivity index for the behavioral results. To do so, we first assume a linear relationship between the BOLD response and neuronal activity [128]. We also assume that the amount of neuronal responses should be proportional to a monotonically increasing function of sensitivity (1/duration threshold). Comparing BOLD responses (Figures 3.8 and 3.9) and the sensitivity index values (Figure 3.10), it is observed that the hMT+ activity better captures the behavioral results. The V1 activity, on the other hand, is not fully consistent with the behavioral results, as we could not observe a significant neural suppression in the narrow attention condition.

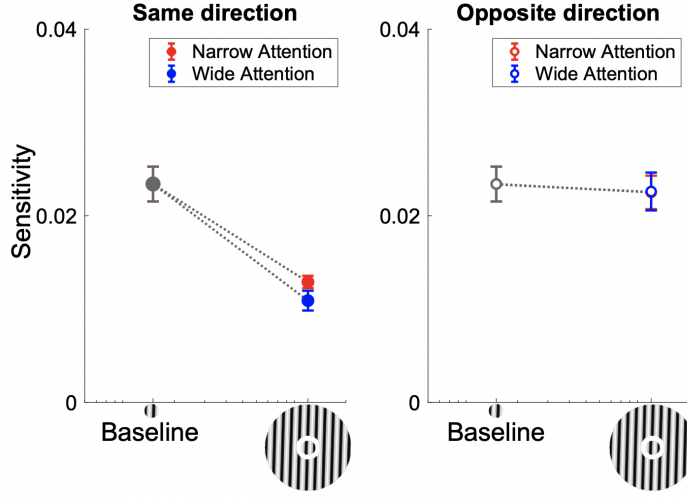


Figure 3.10: Sensitivity values (1/duration threshold). Red and blue lines show averages for narrow and wide attention conditions, respectively. Error bars represent SEM.

Moreover, we tested whether effect of attention as quantified by the difference in SI values between narrow and wide attention conditions (i.e., Attention Index; AI) observed in fMRI results is correlated with the behavioral ones. Since behavioral and hMT+ AIs are normally distributed (Shapiro-Wilk test, $ps > 0.05$) we performed Pearson's correlation analysis and found that the effect of attention in hMT+ is significantly correlated with the attention effect observed in behavioral AI ($r = .78$, $p < 0.05$) in same direction trials (Figure 3.11). Since one data point violated normality assumption for V1 AI, we excluded it and then performed Pearson's correlation and found that it was not significantly correlated with behavioral AI for same and opposite direction trials ($ps > 0.05$) (Figure 3.12).

Considering that asking a second question in the wide attention condition (i.e., whether the center and surround move in the same direction or not) may give rise to the attention effect, we also examined the correlation between the accuracy rate for the second question and the effect of attention as quantified by Attention Index. The accuracy rate for the second question was 70.34 % for same direction trials and 74.4 % for opposite direction trials; however, the accuracy rate of the second question is not significantly correlated with the AI values ($ps > 0.05$).

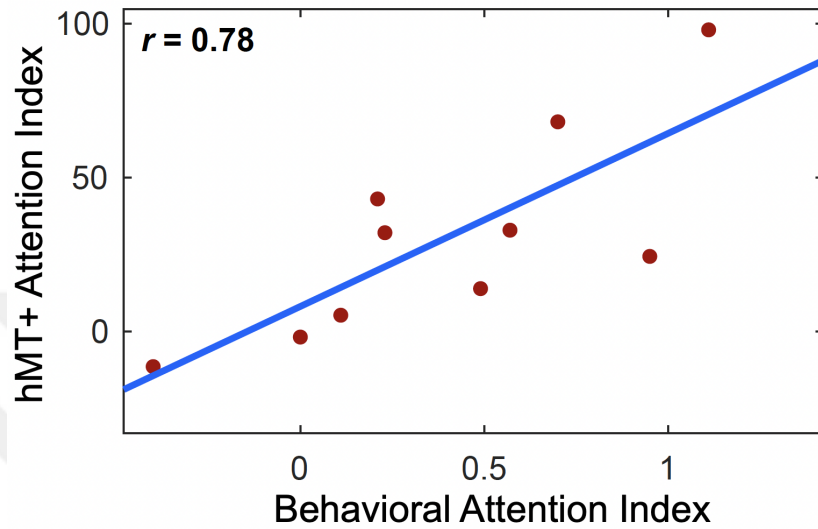


Figure 3.11: Relationship between the effect of attention, defined as the difference in SIs between narrow and wide attention conditions (i.e. Attention Index; AI), observed in fMRI hMT+ and behavioral experiment.

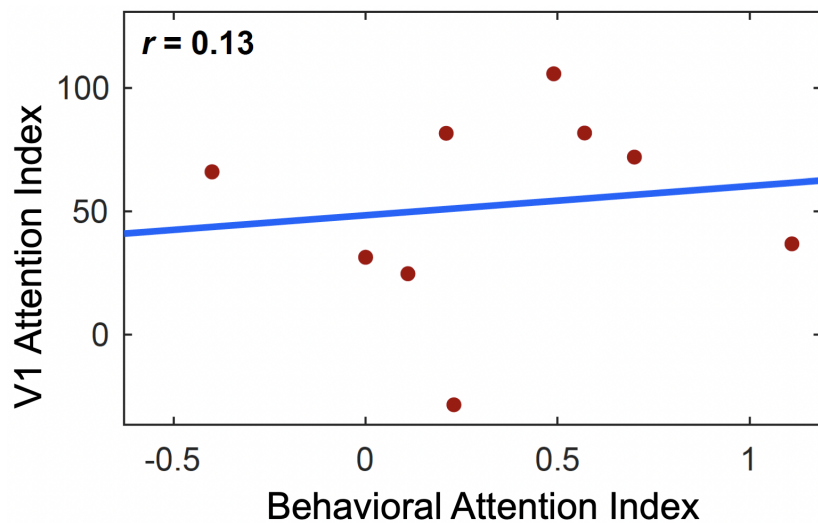


Figure 3.12: Relationship between the effect of attention, defined as the difference in SIs between narrow and wide attention conditions (i.e. Attention Index; AI), observed in fMRI V1 and behavioral experiment.

3.4 Discussion

Here, we examined how the extent of spatial attention affects neural correlates of surround suppression in visual motion processing. First, in a behavioral experiment, we measured motion direction discrimination thresholds while participants were viewing the drifting gratings. In line with our previous behavioral results in Chapter 2, we found that thresholds increased as the spatial extent of attention increased for the same-direction trials. Next, we measured BOLD activity in hMT+ and V1 while participants performed motion direction discrimination tasks as in the behavioral experiment. Our results showed that increasing the spatial extent of attention leads to stronger neural suppression in hMT+, reflecting the perceptual effect. However, although neural suppression in V1 for same-direction trials increased as the spatial extent of attention increased, it did not reach the significance. Further, no effects of either suppression or attention were observed in the opposite-direction trials.

Wider spatial attention leads to stronger surround suppression in hMT+

We show that increasing the spatial extent of attention leads to stronger neural suppression in hMT+. Importantly, this result is consistent with our previous [229] as well as current behavioral results, where we found larger duration thresholds (stronger suppression) under the wide attention condition compared to the narrow attention condition. Besides, it is also in line with previous studies in the literature that show attentional modulation of visual motion processing in MT [240, 241, 211]. For example, Anton-Erxleben and colleagues [211] demonstrated that spatial attention modulates center-surround interactions by changing the RF profile of the MT neurons in the macaque visual cortex. Their results also showed that the strength of the surround suppression increased for the attended location compared to the unattended location by increasing the influence of the attended stimulus on the neuron’s firing rate. These results are in line with our finding of increased surround suppression in hMT+ when participants attend both center and surround gratings, thereby increasing the suppressive influence of the

attended surround on the center. To the best of our knowledge, these results provide the first neural evidence for the effect of the spatial extent of attention on surround suppression.

The general effect of the spatial extent of attention on neural activity in the visual cortex, however, was previously demonstrated in the literature [204, 213]. For example, Itthipuripat and colleagues [204] utilized steady-state visual evoked potentials (SSVEP) to study how varying the spatial scope of attention affected neural activity. They found higher signal-to-noise ratios in focused versus distributed attention conditions, aligning with our observation of higher neural activity (smaller suppression) in narrow versus wide attention conditions in hMT+.

While there was a trend towards increased neural suppression in V1 for same-direction trials as the spatial extent of attention increased, it was not statistically significant. There might be a few possible explanations why the significant effect of attention on suppression is evident in MT, not in V1. First, it might be related to the origins of suppression. If surround suppression in motion perception originates from MT neurons as the MT hypothesis proposes [64], then attention might predominantly affect these neurons, with minimal effect on V1 neurons. Further, recent research [213] supports this idea, revealing that a narrower attentional focus led to a smaller PRF with higher amplitude in the visual cortex, whereas wider attention showed inverse effects. Notably, these attention-driven effects were more pronounced in higher-level visual areas like V3 than in V1 and V2. This aligns with our results, where we found significant attentional modulation in MT but not in V1. It has been known that there are extensive feedback connections from the MT area to V1 [106, 242, 243]. Therefore, current results might reflect the nature of the top-down feedback process of spatial attention. Finally, we used a mixed fMRI design in the current study, which inherently has a lower signal-to-noise ratio compared to block designs. It is possible that the signal is not strong enough to show the effect of attention in V1. A more precise effect might be observed with more data and/or a stronger signal.

Activity of hMT+ neurons better captures perceptual effect

In hMT+, a significant surround suppression effect is observed for both attention conditions, consistent with the behavioral results. Specifically, perceptual sensitivity, as well as cortical responses decreased with size in both attention conditions in same-direction trials. For V1, however, cortical responses significantly decreased with size only in the wide attention condition. These results show that hMT+ activity better captures the perceptual effect. Although existent evidence in the literature also demonstrates decreased MT response with increasing size (i.e., surround suppression) [96, 97, 99, 101], some studies argue this effect could be inherited from V1 [65, 124, 140, 141]. However, in line with our results, a recent fMRI study showed that cortical activity in V1 shows a different pattern of surround modulation compared to hMT+, and the activity of MT but not V1 neurons agrees with the perceptual effect [99]. Furthermore, although some studies found surround suppression in V1, several other studies reported both suppression and facilitation depending on presentation and attention conditions [125, 123]. Taken together, these results suggest hMT+ can be origin of these effects found in current study.

However, it is not possible to rule out the possibility of involvement of V1 area. One possible reason for the absence of surround suppression under the narrow attention condition in V1 is that participants were required to strictly limit their spatial attention to the 1.5° center grating in the narrow attention condition. As we expected, attending to a very small area might reduce the suppressive effect of surround [4] up to a point where surround suppression might have become vanishingly small. Besides, the current results might be due to the technical limitations of the fMRI. Our voxel size is $3 \times 3 \times 3 \text{ mm}^3$, which might be too large to distinguish our V1 sub-ROI activity in response to a small center grating, leading to reduced signal specificity.

Absence of attention and suppression effects when center and surround moved in the opposite direction

Both our behavioral and fMRI results showed that attention has no effect when center and surround gratings drift in opposite directions. This might be related to the absence of surround suppression is observed in opposite direction trials.

On the other hand, the absence of surround suppression in the opposite direction trials is consistent with the literature. For example, both single-unit neural recording studies [39, 104, 221, 222, 223] as well as behavioral studies ([227, 228] showed that surround suppression is reduced or eliminated when surround and center move in opposite directions. Although there are also human fMRI studies reporting that the opposite direction of surround motion facilitates cortical activity for the center [226, 244], they investigated the effect of motion direction using motion aftereffect (MAE) and induced motion paradigms, whereas we used surround suppression phenomena, which might explain the difference in the results.

Chapter 4

Computational Modeling

This chapter is partially based on the publication by Kiniklioglu, M., Boyaci, H. (2022). Increasing spatial extent of attention strengthens surround suppression. *Vision Research*, 199, 108074. <https://doi.org/10.1016/j.visres.2022.108074>. Reproduced (or reproduced in part) based on the author rights provided by Elsevier Publications.

Also, a part of the studies and results presented in this chapter are presented in a preprint by Kiniklioglu, M., Boyaci, H. (2022). Increasing spatial extent of attention strengthens surround suppression, bioRxiv <https://doi.org/10.1101/2021.11.26.470072>

4.1 Introduction

Growing evidence in the literature indicates that the normalization model of attention [4], which incorporates spatial attention into the response normalization of the cortical neurons, can successfully predict the effects of attention on neural and behavioral responses [3, 4, 131, 175, 183, 186, 205, 206, 207, 208, 210]. The model suggests that attention scales the excitatory and inhibitory drives received by a neuron. In the model, the inhibitory drive is spatially broader than the

excitatory drive because it is pooled over a larger number of neurons. Excitatory and inhibitory drives together determine the overall firing rate of that neuron. Accordingly, the spatial spread of attention field affects the contrast-response functions of neurons and, consequently, behavioral sensitivity. Specifically, the model predicts that a narrower attention field causes weaker suppression because it primarily increases the effect of the excitatory drive. Conversely, a wider attention field leads to stronger suppression because it increases both the effects of excitatory and inhibitory drives. Indeed, several single-unit recording studies have been suggested to be consistent with the predictions of the normalization model [183, 186, 210]. For instance, surround suppression was stronger when attention was directed to the RF surround than to the RF center. Likewise, several behavioral results can be explained within the normalization framework [3, 98, 204].

The success of the normalization model in explaining the effect of spatial attention on surround suppression has led us to use the model to establish a link between our behavioral results in Chapter 2 and the response characteristics of visual neurons. To do so, we performed computer simulations using parameters derived from the MT area of the cortex. Furthermore, we simulated cortical responses in hMT+ and V1 to test if the model accounts for our empirical findings in Chapter 3.

4.2 Methods

The model simulates the response of a population of neurons that are tuned to spatial position (spatial attention) and motion direction (feature-based attention). The model has three components:

1. Stimulus Drive, which represents the excitatory input a neuron receives;
2. Suppressive Drive, which represents the summed activity of a pool of neurons;

3. Attention Field, which modulates attentional gain for each neuron in the population according to spatial position and direction tuning (see Figure 4.1).

To determine the population response, the stimulus drive is multiplied by the attention field and then divided by the suppressive drive. The model can be summarized by the following equation:

$$R(x, \theta, c) = \frac{E(x, \theta, c) \times M(x, \theta, M_g)}{S(x, \theta, c) + \sigma}, \quad (4.1)$$

where R is the predicted population response as a function of spatial position (x), direction (θ), and contrast (c). E and S are the excitatory and suppressive drives respectively, and σ is the semi-saturation constant, which prevents R from being undefined when S equals zero. Excitatory drive, E , is computed by the following equation:

$$E(x, \theta, c) = e(x_e, \theta_e) * N(x, \theta, c), \quad (4.2)$$

where e is a two-dimensional (2-D) Gaussian function with the spatial position (x_e) and the direction (θ_e) that determines spatial and direction tuning, respectively, for the excitatory drive (E), $*$ denotes convolution and N is the neural representation of the stimulus, which is also a 2-dimensional Gaussian function with the stimulus position (x), and the direction (θ), and scaled by the contrast (c).

Suppressive drive, S , is computed by the following equation:

$$S(x, \theta, c) = s(x_s, \theta_s) * \left(E(x, \theta, c) \times M(x, \theta, M_g) \right) \quad (4.3)$$

where s is another 2-D Gaussian function as e , but shows broader tuning in spatial position (x_e) and direction (θ_s). M represents the attention field, which reflects how spatial attention modulates the stimulus processing by scaling E . M is a 2-D Gaussian function whose spatial extent is set by the attentional gain factor M_g . The operator “ $\times$ ” represents element-wise multiplication (Hadamard product).

We computed predicted motion discrimination thresholds from model responses as

$$T = \frac{C}{R_{peak}}, \quad (4.4)$$

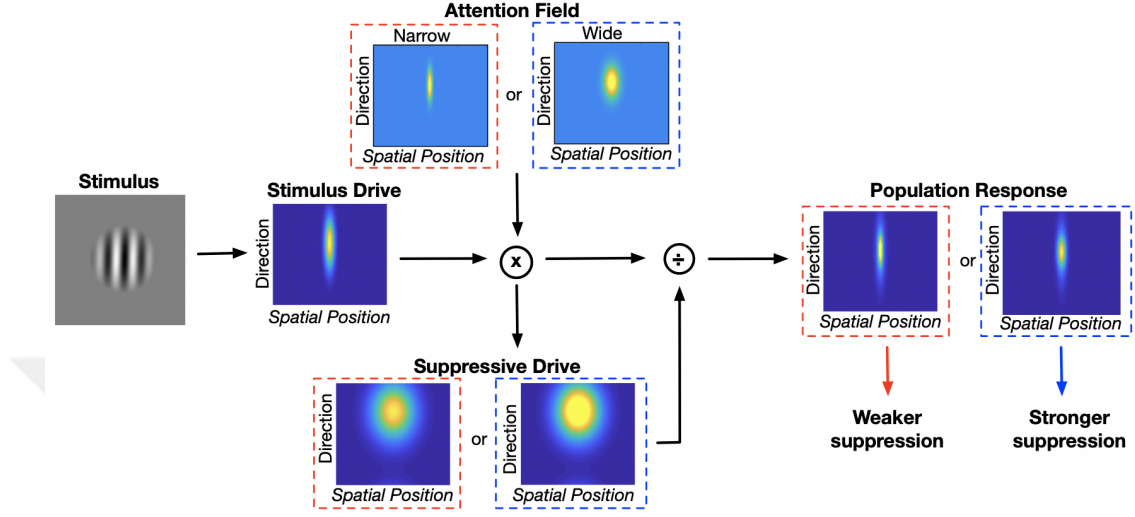


Figure 4.1: A schematic representation of the normalization model of attention. Stimulus Drive is multiplied by the attention field, then normalized by the Suppressive Drive to determine population response. We simulated model responses using a narrow attention field for the narrow attention condition (red dashed squares) and a wider attention field for the wide attention condition (blue dashed squares) (Eqs. 4.1- 4.3).

where R_{peak} is the maximum of the predicted model response R [99, 98, winner-take-all approach, see] and C is a constant linking the thresholds and neuronal responses [98].

Since our stimulus consisted of a center grating surrounded by an annular grating, the neural representation of this stimulus, N , is obtained by the summation of the two 2-D Gaussian functions corresponding to the neural representation of the center grating and the annular grating. Specifically, the annular grating was modeled by subtracting a full 2-D Gaussian whose size corresponds to the outer diameter of the small gap between the center and surround grating (2.8°) from another full 2-D Gaussian whose size corresponds to the outer diameter of the annular grating (5.3° or 12°).

To model the neural responses to the narrow and wide attention conditions, we used a smaller (M_g , 3 arbitrary units) and larger (M_g , 9 arbitrary units) spatial attention width, respectively (Figure 4.1). Moreover, the opposite direction trials are modeled by using a surround stimulus direction that is 180° away from the

direction of the center. To be more specific, the stimulus direction parameter for the 2-D Gaussian function was -90° for the center and 90° for the surround [4, 229].

To stimulate behavioral thresholds, we used parameters that characterize MT neurons because previous literature suggests that the neuronal activity in the (h)MT area can successfully explain the size-contrast interaction in motion discrimination, both at the behavioral [97, 98] and neuronal levels [3, 97, 99, 202]. To stimulate fMRI responses in V1 and (h)MT, we used parameters that characterize V1 and MT neurons, respectively, based on studies reporting results of single-unit cell recordings from the monkey visual cortex.

Although feature-based attention was not the focus of the current study, the same versus opposite direction of motion incidentally introduced feature-based attention as a factor in our design. In the normalization model of attention, the attention field is not only selective for a specific position (spatial attention) but also for the direction of motion (feature-based attention). Hence, to address this possible effect, we included a feature-based attention component in the model (Figure 4.1).

Table 4.1 reports the parameters used in simulations for behavioral experiment that were chosen based on the receptive field properties of the MT neurons reported in the literature [97, 98, 99]. Critically, we used parameters that characterize MT neurons because previous literature suggests that the neuronal activity in the (h)MT area can successfully explain the size-contrast interaction in motion discrimination, both at the behavioral [97, 98] and neuronal levels [3, 202, 97, 99]. Table 4.2 reports the parameters used in simulations for the fMRI experiment that were chosen based on the receptive field properties of the V1 and MT neurons [97, 98, 99]. Simulations were done on Matlab 2019b, separately for same-direction and opposite-direction trials. The model was implemented using custom MATLAB functions [98, 99].

Table 4.1: Normalization model parameters for simulating behavioral results.

Symbol	Description	MT
c	Stimulus contrast	0.03 or 0.98
x_e	Excitatory spatial pooling width	4 (a.u.)
x_s	Suppressive spatial pooling width	40 (a.u.)
θ_e	Excitatory direction pooling width	25°
θ_s	Suppressive direction pooling width	50°
σ	Semi-saturation constant	0.0002 (a.u.)
M_g	Spatial width of attention field	3 or 9 (a.u.)

Table 4.2: Normalization model parameters for simulating fMRI results.

Symbol	Description	MT	V1
c	Stimulus contrast	0.98	0.98
x_e	Excitatory spatial pooling width	4 (a.u.)	2 (a.u.)
x_s	Suppressive spatial pooling width	40 (a.u.)	6 (a.u.)
θ_e	Excitatory direction pooling width	25°	5°
θ_s	Suppressive direction pooling width	50°	10°
σ	Semi-saturation constant	0.0002 (a.u.)	0.0002 (a.u.)
M_g	Spatial width of attention field	3 or 9 (a.u.)	3 or 9 (a.u.)

4.3 Results

4.3.1 Model Results for Behavioral Experiment

First, we performed simulations to test whether the model could predict the behavioral results presented in Chapter 2. Figure 4.2 shows the simulation results. Simulation results based on MT parameters are qualitatively similar to the behavioral findings shown in Figure 2.3, in Chapter 2. Specifically, simulated thresholds are lower with a small attention field compared to those with a large attention field, which is consistent with the weaker surround suppression under the narrow compared to the wide attention condition that we found in the behavioral experiment.

Besides, our model predicts that thresholds increase as the attention field increases, not only for the same-direction trials but also for the opposite-direction trials. Furthermore, the model predicts that the increase in surround suppression with a larger attention field is weaker in opposite-direction trials compared to same-direction trials, which is also consistent with the behavioral data. On the other hand, simulation results based on V1 parameters are not fully consistent with behavioral data. These results show that the behavioral effect of attention on surround suppression can be explained by a divisive normalization framework, which is in line with the neuronal suppression observed in hMT.

4.3.2 Model Results for the fMRI Experiment

Next, we tested whether our fMRI results could be accounted for by the model that incorporates the effect of spatial attention into the normalization model [4]. Here, we first tested whether the normalization model could explain our pre-fMRI behavioral threshold measurements. To simulate the trials under the wide and narrow attention conditions, we simply used a wider and a narrower attention field, respectively (Figure 4.1).

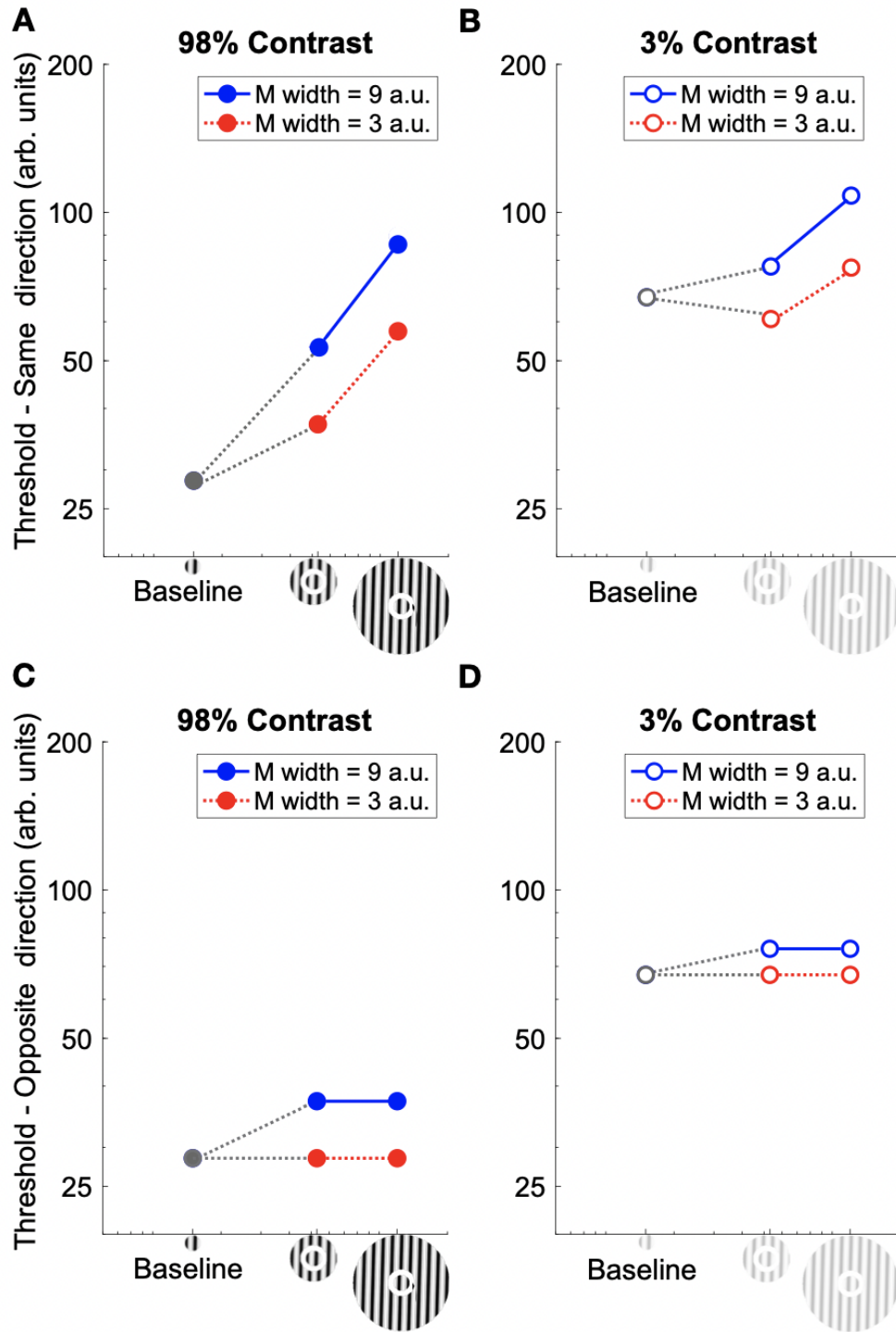


Figure 4.2: Model simulation results for behavioral experiment based on parameters from MT neurons. Predictions of the normalization model for the same-direction trials (A and B) and opposite-direction trials (C and D).

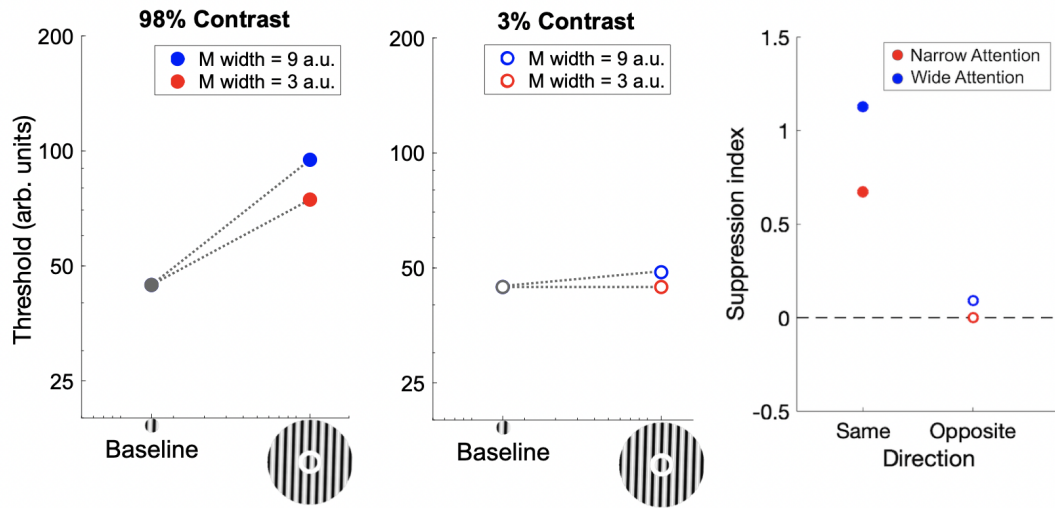


Figure 4.3: Model simulation results for the pre-fMRI behavioral experiment. Predictions of the normalization model for the same- and opposite-direction trials, based on parameters from MT neurons.

Simulation results are shown in Figure 4.3. The results of the model are qualitatively similar to our behavioral findings (see Figure 3.7) in Chapter 3. Specifically, we found that using a larger attentional gain factor within our model led to larger motion discrimination thresholds that closely mirrored our observation of stronger surround suppression in the wide attention condition. Furthermore, the model also predicts a smaller, if any, effect of attention on surround suppression in opposite-direction trials, which is also consistent with the behavioral data.

Then, we examined whether the normalization model could describe the effect of spatial attention on neural suppression in hMT+ and V1. Simulation results based on parameters that characterize MT and V1 neurons are shown in Figures 4.4 and 4.5, respectively. Again, simulation results are in good agreement with our empirical data (Figures 3.8 and 3.9), especially for the same-direction trials. These results suggest that the effect of attention on surround suppression can be explained within a divisive normalization framework.

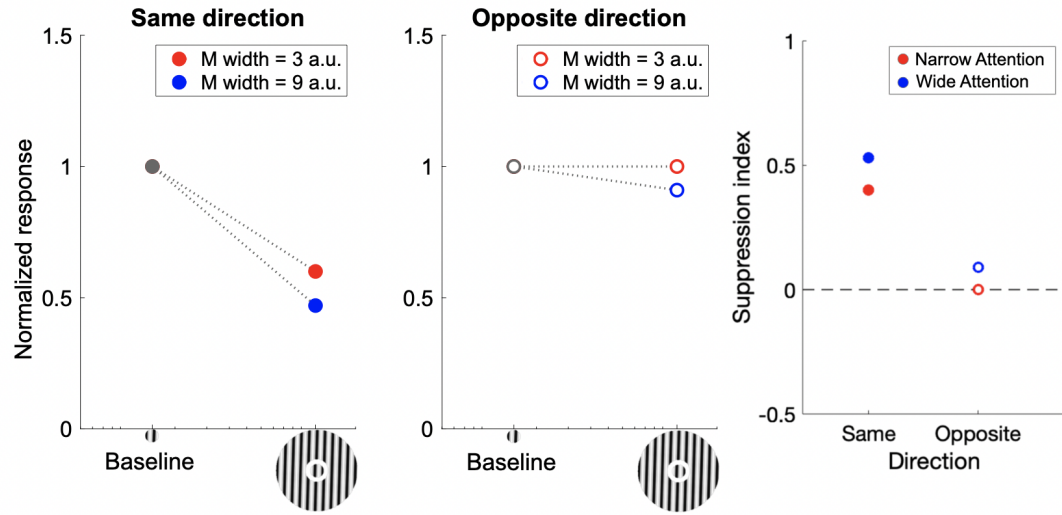


Figure 4.4: Model results for the fMRI BOLD response based on parameters that characterize MT neurons.

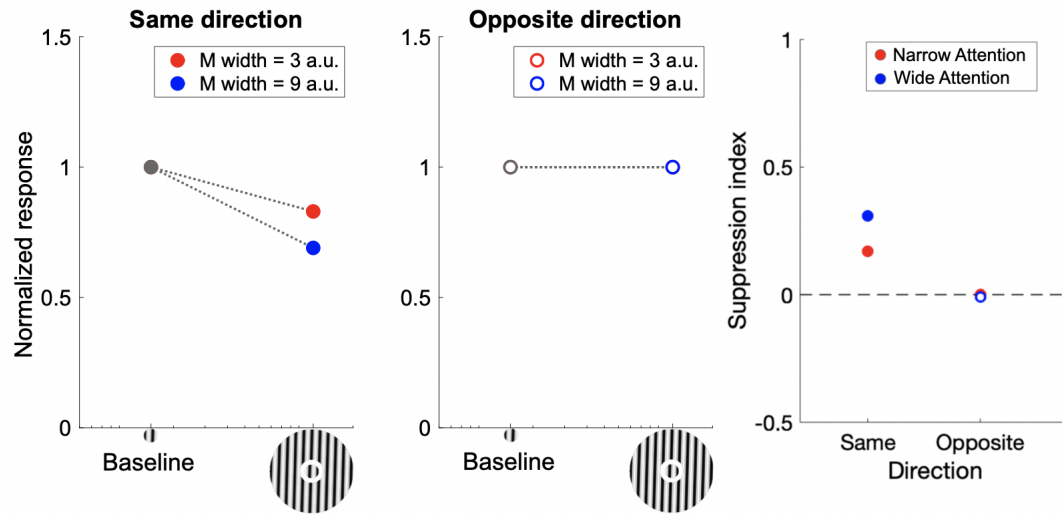


Figure 4.5: Model results for the fMRI BOLD response in V1 based on parameters that characterize V1 neurons.

4.4 Discussion

Here we performed computer simulations using the normalization model of attention with MT parameters to establish a link between our behavioral results and possible neuronal mechanisms, as previously done in the literature [97, 99]. Our simulations showed that using smaller versus larger multiplicative attentional gain in the model can successfully predict the observed behavioral results both for the same-direction and opposite-direction trials. These results suggest that neuronal suppression in hMT+ might explain the perceptual effect of attention on surround suppression. This supports the hypothesis that the behavioral manifestation of surround suppression in motion perception originates in hMT [97, 64, 101, 245].

Furthermore, we simulated cortical responses in MT and V1 to test if the model accounts for our empirical findings in Chapter 3. We found that the normalization model of attention [4] can predict the effect of attention on BOLD fMRI responses in hMT+ and V1. These findings, together with the results of the behavioral and fMRI experiments discussed in Chapters 2 and 3, respectively, revealed the critical role of spatial attention on surround suppression and showed that the model provides a parsimonious account for the effect of spatial attention within the context of surround modulation.

One limitation of the normalization model is that it doesn't enable rigorous model comparisons. While the model has proven useful in explaining various phenomena such as surround suppression and attentional modulation [4] and offers an intuitive framework for understanding complex neural and behavioral interactions, it is difficult to validate its assumptions or directly compare it against alternative models. Furthermore, the model allows for qualitative rather than quantitative comparisons with empirical data, making it difficult to statistically evaluate its precision.

Chapter 5

General Discussion and Future Directions

Behavioral and neural sensitivity to a visual stimulus often depends on the spatial context in which the stimulus is seen. For example, spatial attention has well-documented effects on center-surround interactions in visual processing [183, 186]. Specifically, spatial attention is known to modulate surround suppression both in humans [3, 123, 209, 122] and non-human animals [131, 175, 183, 186]. However, no previous study has directly and systematically investigated the effect of the spatial extent of attention on surround suppression in human motion perception. This dissertation aimed to unravel the effect of the extent of spatial attention on center-surround interaction in visual motion processing. In Chapter 2, I present my results on the duration thresholds for discriminating the motion direction of foveally presented drifting gratings under wide and narrow spatial attention conditions. First, we found that increasing the spatial extent of attention evoked stronger surround suppression. Second, the magnitude of the effect increased as the surround size increased for low-contrast stimuli but did not change for high-contrast stimuli. Third, attention had a weaker effect when the center and surround gratings drifted in opposite directions.

In Chapter 3, to understand the cortical mechanism that underlies the attentional modulation of surround suppression, we investigated how the BOLD fMRI response associated with surround suppression in hMT+ and V1 changes depending on the spatial extent of attention. First, we measured motion direction discrimination thresholds in a pre-fMRI behavioral experiment while participants were viewing the drifting gratings. In line with our previous behavioral results in Chapter 2, we found that thresholds increased as the spatial extent of attention increased for the same-direction trials. Next, we measured BOLD activity in hMT+ and V1 while participants were performing motion direction discrimination task as the behavioral experiment. We found that increasing the spatial extent of attention leads to stronger neural suppression in hMT+ activity, reflecting the perceptual effect. The pattern of V1 activity, on the other hand, was not fully consistent with the behavioral effect. Further, neither attention nor suppression effects were observed when the center and surround drifted in opposite directions.

To establish a link between our behavioral results in Chapter 2 and the response characteristics of V1 and MT neurons, in Chapter 4, we performed computer simulations using parameters derived in literature from MT area. Our simulations showed the model can successfully predict the observed behavioral results both for the same-direction and opposite-direction trials. Furthermore, we simulated cortical responses in hMT+ and V1 and found that the model [4] can predict the effect of attention on BOLD fMRI responses in hMT+ and V1. The following sections discuss the interpretations, implications, and potential applications of these findings within the theoretical framework.

5.1 Wider spatial attention leads to stronger surround suppression

The behavioral findings in Chapter 2 showed that surround suppression was significantly stronger under the wide-attention condition compared to the narrow-attention condition. This is consistent with previous studies in the literature where the modulatory effect of attention on surround suppression has been commonly demonstrated using a paradigm in which observers are asked to attend versus ignore a static stimulus [3, 123, 224, 225]. However, unlike in previous studies, here we investigated the effect of the spatial extent of attention rather than the mere presence or absence of spatial attention. Hence, to the best of our knowledge, our results are the first to systematically demonstrate that surround suppression in motion perception becomes stronger with a wider attention field.

It could also be argued that our results were observed because attention increases the effective stimulus contrast [189, 190, 191, 246]. Given that surround suppression depends on contrast, it is possible that under the wide attention condition, the effective contrast of the surround increases, making it exert a more suppressive effect on the center [247, 248]. Note that the normalization model of attention would also predict an increase in effective contrast. Thus, in a way, both effects, i.e., an increase in surround suppression and an increase in effective contrast, may arise from the same neuronal mechanisms.

In Chapter 3, we show that increasing the spatial extent of attention leads to stronger neural suppression in hMT+. Importantly, this result is consistent with our previous [229] as well as current behavioral results, where we found larger duration thresholds (stronger suppression) under the wide attention condition compared to the narrow attention condition. To the best of our knowledge, these results provide the first neural evidence for the effect of the spatial extent of attention on surround suppression. Although there is limited information in the literature on the effect of the spatial extent of attention on neural activity in the visual cortex, our results are in line with the studies showing a higher neural activity in the visual cortex during the focused attention condition compared to

the distributed attention condition, mirroring our finding of smaller suppression in the narrow attention condition compared to the wide attention condition in hMT+ [204, 213].

Moreover, considering the extensive feedback connections from MT to V1 [106, 242, 243], the more pronounced attentional modulation found in hMT+ could be indicative of the top-down feedback mechanisms of spatial attention. Consistent with this idea, a recent research showed that effect of spatial extent of attention were more pronounced in higher-level visual areas (V3) than lower ones (V1, V2) [213], which aligns with our results. Consequently, current results might reflect the nature of the top-down feedback process of spatial attention.

5.2 Activity of hMT+ neurons better captures the perceptual effect

While perceptual sensitivity and cortical responses in hMT+ decrease with size in both attention conditions, cortical responses in V1 decrease only in the wide attention condition. Hence, neural activity in hMT+ is more consistent with both surround suppression and attention effects observed in behavioral results, which may suggest that activity in hMT+ may reflect the cortical mechanisms underpinning these perceptual effects. This is consistent with prior fMRI studies showing that hMT+ activity mirrors behavioral outcomes of surround suppression [96, 97, 99]. Moreover, in Chapter 4, our model simulations using MT parameters can successfully predict the observed behavioral results, which provide further evidence that the perceptual consequences of surround suppression in motion perception likely originate in hMT+ [64, 97, 101].

However, we cannot completely rule out the potential involvement of the V1 area. One possible reason for the absence of surround suppression under the narrow attention condition in V1 is that participants were required to strictly limit their spatial attention to the 1.5° center grating in the narrow attention

condition. As we expected, attending to a very small area might reduce the suppressive effect of surround [4] up to a point where surround suppression might have become vanishingly small. Besides, the current results might be due to the technical limitations of the fMRI. Our voxel size is $3 \times 3 \times 3 \text{ mm}^3$, which might be too large to distinguish our V1 sub-ROI activity in response to a small center grating, leading to reduced signal specificity.

5.3 Spatial attention has a weaker effect when center and surround move in the opposite direction

Although there is limited information in the literature on the behavioral effects of surround suppression when center and surround move in opposite directions [138, 139, 226, 227, 228], our behavioral results from Chapter 2 are in line with the studies showing that surround suppression is more pronounced in low contrast but reduced for high contrast, especially in large surrounds [138, 228].

While our behavioral and fMRI results in Chapter 3 showed that spatial attention has no effect when center and surround gratings move in opposite directions, this is not unexpected, considering the absence of surround suppression in opposite-direction trials. In fact, it is consistent with both neural recording and behavioral studies, which have often reported reduced or absent surround suppression under such conditions [39, 104, 221, 222, 227]. Previous fMRI studies suggested that opposite-direction surround motion enhances cortical activity [226, 244], but differences in experimental design, specifically in stimulus configuration and the use of different paradigms like MAE and induced motion, may account for the discrepancy between our findings and those of earlier studies.

5.4 Clinical populations, surround suppression, and spatial attention

Weaker surround suppression has been observed in various clinical conditions such as schizophrenia [100], major depressive disorder [142], and autism spectrum disorder (ASD) [98, 102, 143]. The underlying causes of this interesting phenomenon are still debated. Previously, a weaker GABAergic system in the patients was put forward to explain the findings [100]. GABA is known to critically modulate lateral inhibitory interactions in the visual cortex, and GABAergic deficits have been reported in old age, schizophrenia, and depression [149, 150, 151]. It is hypothesized that an abnormal decrease in GABA concentration in the visual cortex might lead to decreased cortical inhibition, which, in turn, leads to weaker surround suppression. However, this hypothesis was not supported by more recent MR spectroscopy studies [97].

On the other hand, it is well known that attention mechanisms are affected under many clinical disorders [249, 250, 251, 252]. It is possible that abnormal attention leads to abnormal surround suppression in these patients. In line with this conjecture, in a recent study, Schallmo and colleagues [98] found weaker suppression in ASD patients and suggested that this could be because of narrower spatial attention. Moreover, an increased level of acetylcholine, a neuromodulator thought to be critically involved in attentional processing by leading to more focused voluntary spatial attention, is reported to result in weaker surround suppression [253]. Thus, we contend that attention may provide an alternative explanation for the abnormal surround suppression found in clinical populations.

5.5 Normalization model of attention can explain the results

In Chapter 4, we used the normalization model of attention [4] to show that neuronal suppression in hMT could account for the perceptual effect of attention on surround suppression, supporting the MT hypothesis [97, 64, 101, 245]. We support this prediction with empirical evidence in Chapter 3, where we found stronger surround suppression in hMT+ under the wide attention condition. Importantly, our results show that a simple computational model can qualitatively predict the behavioral effects of surround suppression for various factors like contrast, size, motion direction, and attention, which paves the way for future studies.

Moreover, we simulated cortical responses in hMT+ and V1 and found that neural correlates of attention on surround suppression could be explained by the NMA, as previously done in the literature [3, 183, 186]. Taken together, the normalization model, which is an important tool to establish a link between the perceptual effect of surround suppression and the response characteristics of the visual neurons, could account for behavioral and neural correlates of the effect of spatial attention on surround suppression.

Here we found that a model incorporating multiplicative attention gain into the normalization model can successfully explain the experimental data. Whereas some previous studies that investigated the effect of attention on target-context interactions argued that the attention gain could be additive [254, 255]. The difference between our findings could be because of the differences in stimulus configuration and experimental design. Most notably, in both studies, targets and contextual elements were spread across a wide region in the visual field. Further, the attention manipulations were different in these studies. In the study of Poltoratski and colleagues [254], spatial cues were used to shift attention to either one of the two closely spaced target locations in opposite hemifields. This could have restricted the attention field on the target more severely than in our design. In the study of Schallmo and colleagues [255], one of the comparisons was between fMRI BOLD responses while attending targets and performing a

demanding fixation task. In our study, on the other hand, a single target and its surround were closely positioned, and attention was spread over either only the target or the target and its surround. These factors could have led to the differences between our study and those earlier studies [254, 255].

5.6 Limitations and Future Directions

When we compare the results of opposite-direction trials in the behavioral experiment in Chapter 2 and the pre-fMRI behavioral experiment in Chapter 3, it is clear that surround suppression disappears, and therefore the effect of spatial attention disappears in the pre-fMRI behavioral experiment. The absence of the effect could be attributed to individual differences among participants. Different cohorts or variations in individual sensitivity in the same cohort could lead to inconsistencies in results. Also, there is a clear trend in the results of behavioral experiment that surround suppression decreases in high-contrast opposite-direction trials as the size of the surround increases. This is actually in line with the results of behavioral studies, which show that when the center and surround move in the opposite direction, surround suppression is reduced or eliminated in high-contrast trials for large-surround conditions [138, 139, 226, 227, 228].

Moreover, under the limiting conditions of the pandemic, some of the participants needed to participate in all the versions of the experiments for this study, including the pilot, behavioral, and fMRI experiments. Therefore, they might have gotten better at increasing their attention field width as they are more trained compared to participants who only participated in the fMRI experiment, which could cause variability in the data. To eliminate such confounds in future studies, attentional training before the experiments must be provided to ensure that all participants can widen their attention fields.

As stated previously, abnormal surround suppression is observed in many clinical disorders [98, 100, 102, 142, 143]. Therefore, tests of surround suppression can be used as a tool to understand the neural basis of abnormal visual processing

and might shed light on the dynamics of clinical conditions. However, to compare with the clinical populations and better understand the role of spatial attention in abnormal vision, the effect of attention should be characterized in neurotypicals first. Here, we characterized the effect of the spatial extent of attention on human motion perception by utilizing the surround suppression phenomenon in neurotypical participants. Hence, as a next step, our experimental design can be used to investigate the role of attention mechanisms in visual processing in clinical populations in future studies. Considering that attention mechanisms are affected by many clinical disorders [249, 250, 251, 252], abnormal attention may lead to abnormal surround suppression in the patients mentioned above. Therefore, to test this hypothesis, how surround suppression is affected by the spatial extent of attention should be investigated in clinical populations as well. If these patients have, for example, smaller attention fields, we would not expect a significant difference in the strength of the surround suppression between narrow and wide attention conditions, as patients already have difficulty enlarging them [98].

As stated earlier, while some results in the literature support the response gain [185, 195], other findings show a response pattern similar to contrast gain [187, 193, 203]; or in between response and contrast gain [194], and the normalization model of attention can explain this complex pattern of results. The model suggests attending to an area larger than the stimulus size results in contrast gain, whereas attending to an area smaller than the stimulus size results in response gain [4]. The results of human psychophysics experiments show expected shifts in contrast-response function similar to contrast and response gain depending on the spatial extent of attention [3, 204]. In the current study, our experimental design is not adequate to draw conclusions about the plausibility of the contrast gain vs. response gain mechanisms, as our main comparison is based on attending to a smaller vs. larger area and not attending or ignoring the stimulus. Moreover, only two contrast levels (3% and 98%) are used in the current study, which makes it hard to discuss how contrast-response functions change depending on spatial attention. To answer this question, we need more contrast levels to calculate contrast-response functions to see if there is an upward shift of the contrast-response function indicating response gain or a leftward shift

of the contrast-response functions indicating contrast gain [3, 4]. Therefore, in future studies, multiple contrast levels should be used to determine whether the results are due to response gain, contrast gain, or both.

Our results demonstrated that hMT+ activity better captures the pattern of the behavioral results, suggesting that hMT+ is a likely origin of the effect. However, we cannot completely rule out the possibility of involvement of the V1 area. To directly test this idea, multivoxel pattern analysis (MVPA) could be used to assess how accurately the direction of motion can be predicted based on the patterns of neural activity in hMT+ and V1. Likewise, effective connectivity analysis can be employed to understand how top-down effect of spatial attention modulates V1 and hMT+ activity and whether such modulations differ across two regions.

5.7 Conclusion

To conclude, in this study, we demonstrated that the extent of spatial attention affects the perceptual and neural correlates of center-surround interaction in human motion processing. Our findings showed that increasing the spatial extent of attention evokes stronger suppression at a perceptual level and also in hMT+ area of the cortex. However, this was not the case for the activity in V1. Then, we showed that the normalization model of attention [4] can successfully predict the response patterns in hMT+ and V1. Furthermore, the model could provide a link between cortical responses and behavioral thresholds. Overall, our findings and analyses showed that the behavioral effect can be successfully predicted by hMT+ activity. These results reveal the critical role of spatial attention on surround suppression, namely that surround suppression in motion perception becomes stronger with a wider attention field, and reveal possible cortical mechanisms underpinning the effect. Further, these results also suggest that the reduced surround suppression found in certain clinical disorders (e.g., schizophrenia and autism spectrum disorder) may be caused by abnormal attention mechanisms.

Appendix A

Psychometric Function Fits in Behavioral Experiments

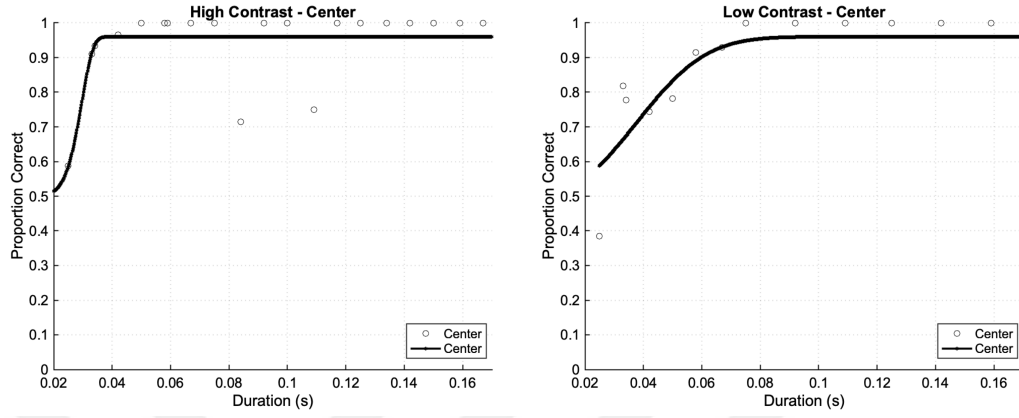


Figure A.1: Weibull function fits for a single participant (1) for center-only condition.

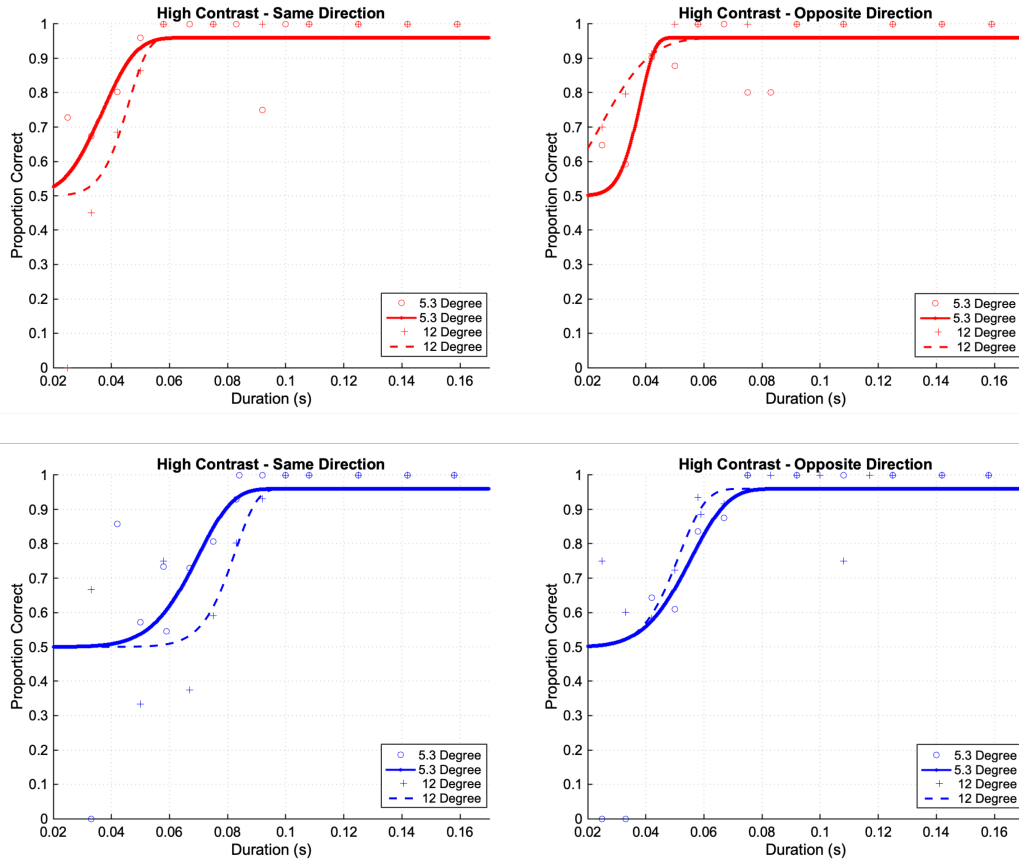


Figure A.2: Weibull function fits for a single participant (1) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

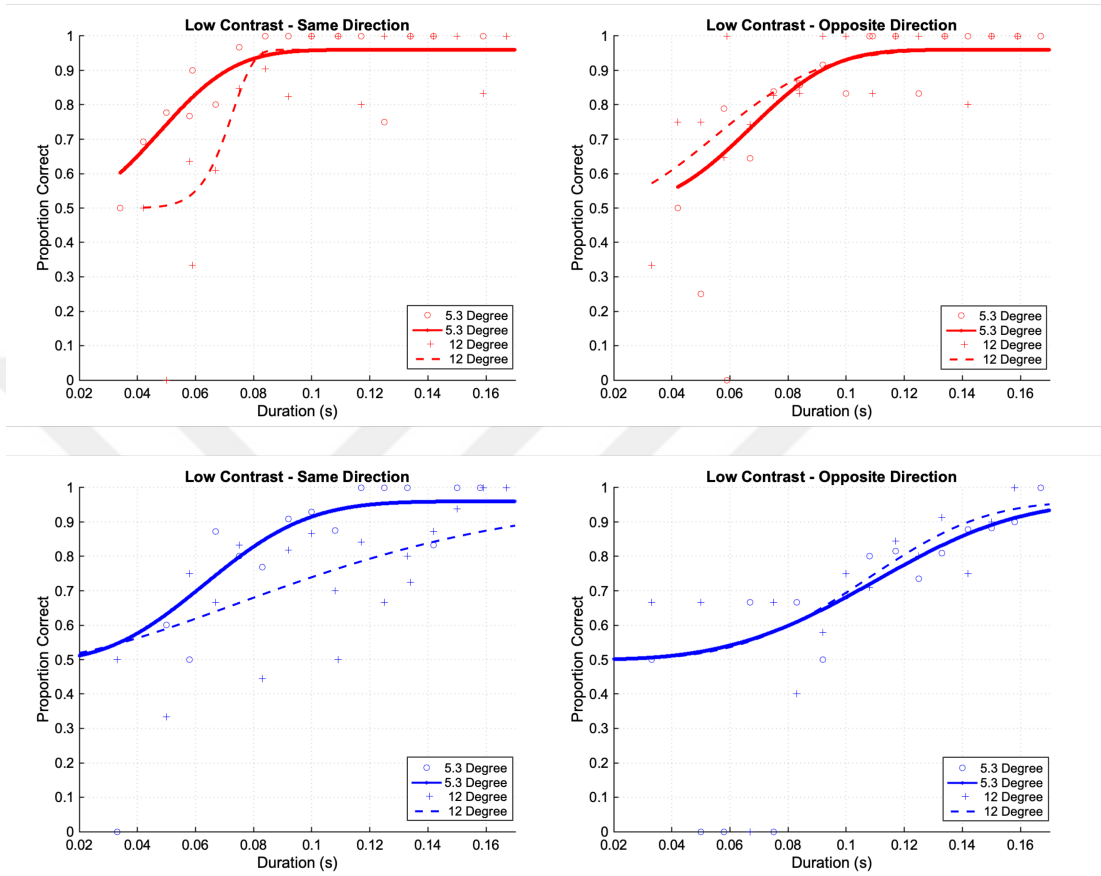


Figure A.3: Weibull function fits for a single participant (1) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

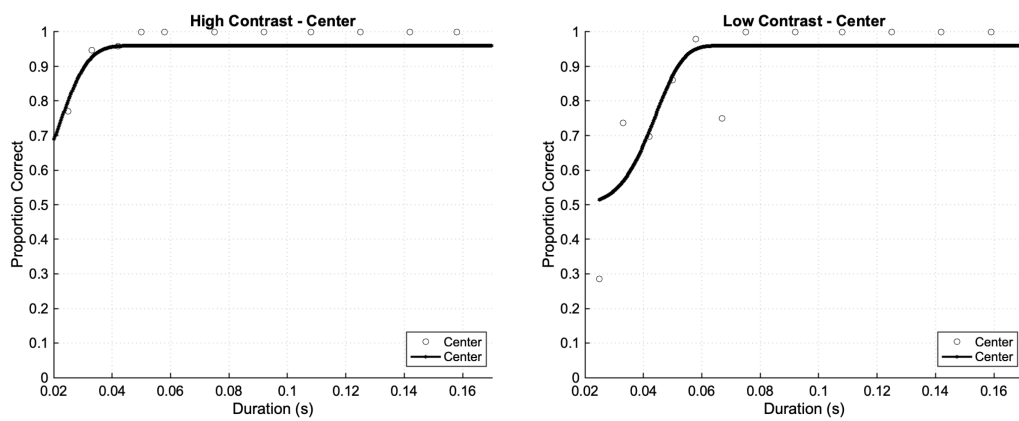


Figure A.4: Weibull function fits for a single participant (2) for center-only condition.

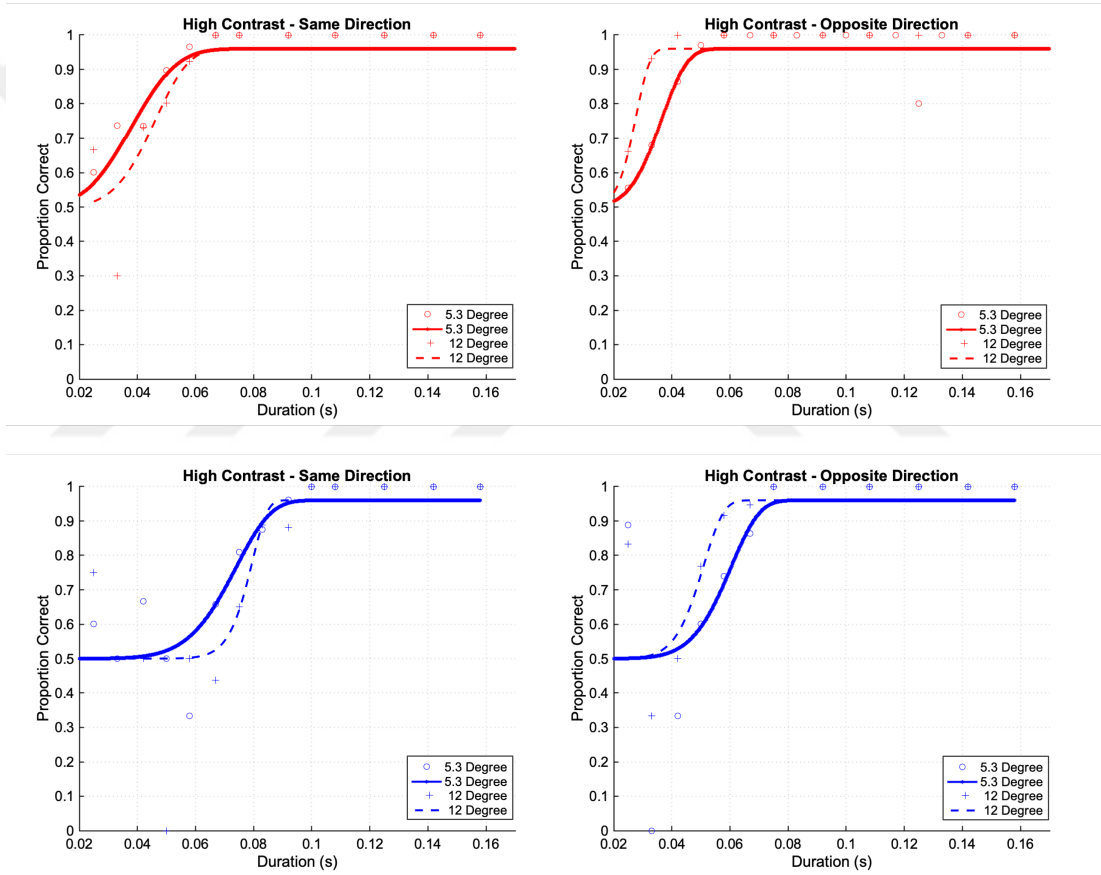


Figure A.5: Weibull function fits for a single participant (2) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

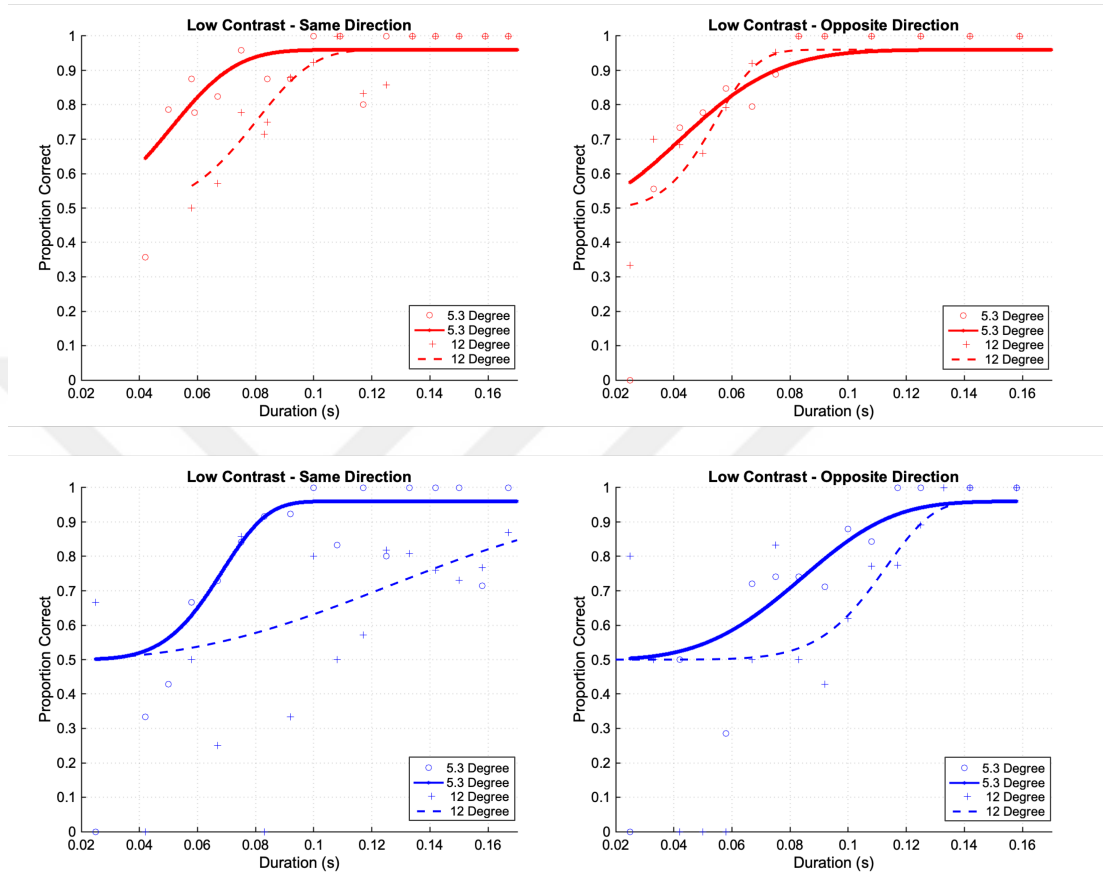


Figure A.6: Weibull function fits for a single participant (2) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

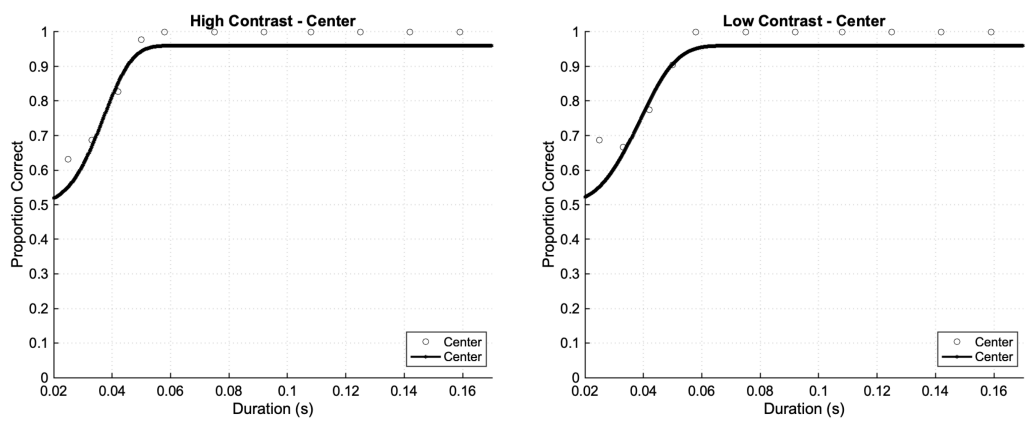


Figure A.7: Weibull function fits for a single participant (3) for center-only condition.

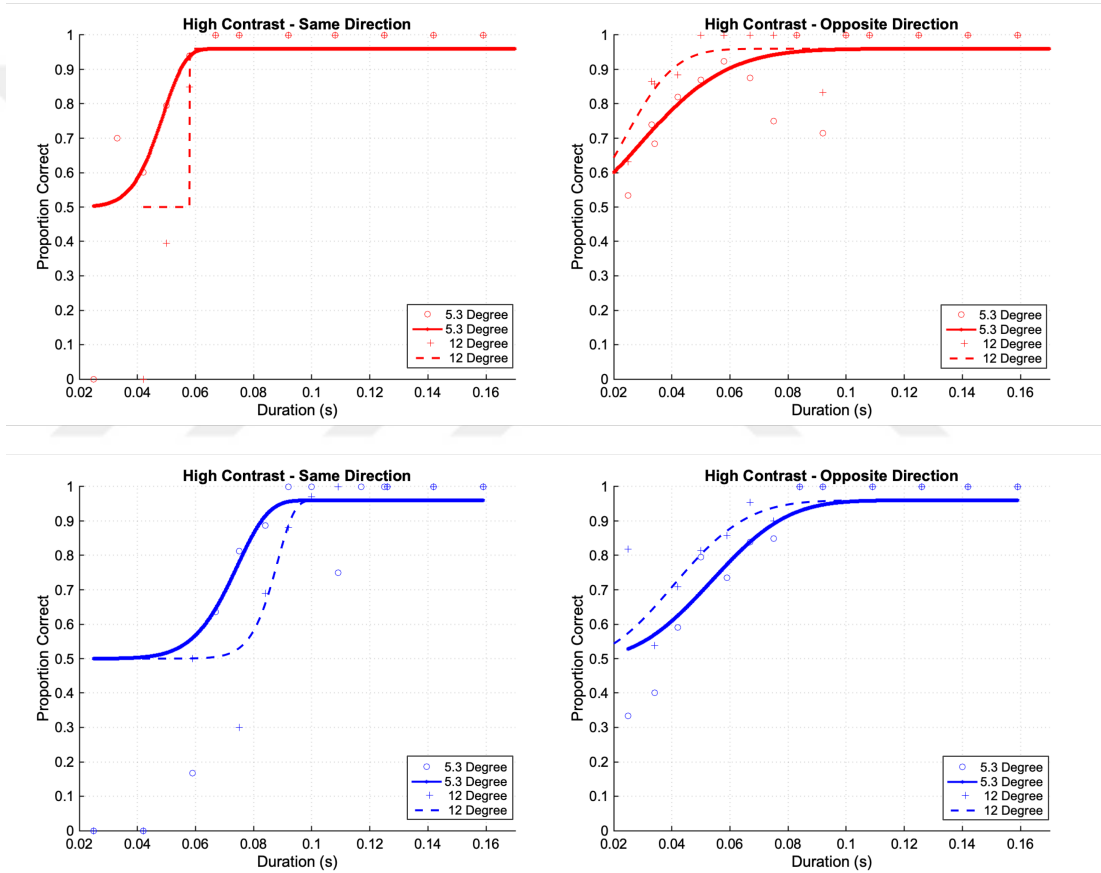


Figure A.8: Weibull function fits for a single participant (3) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

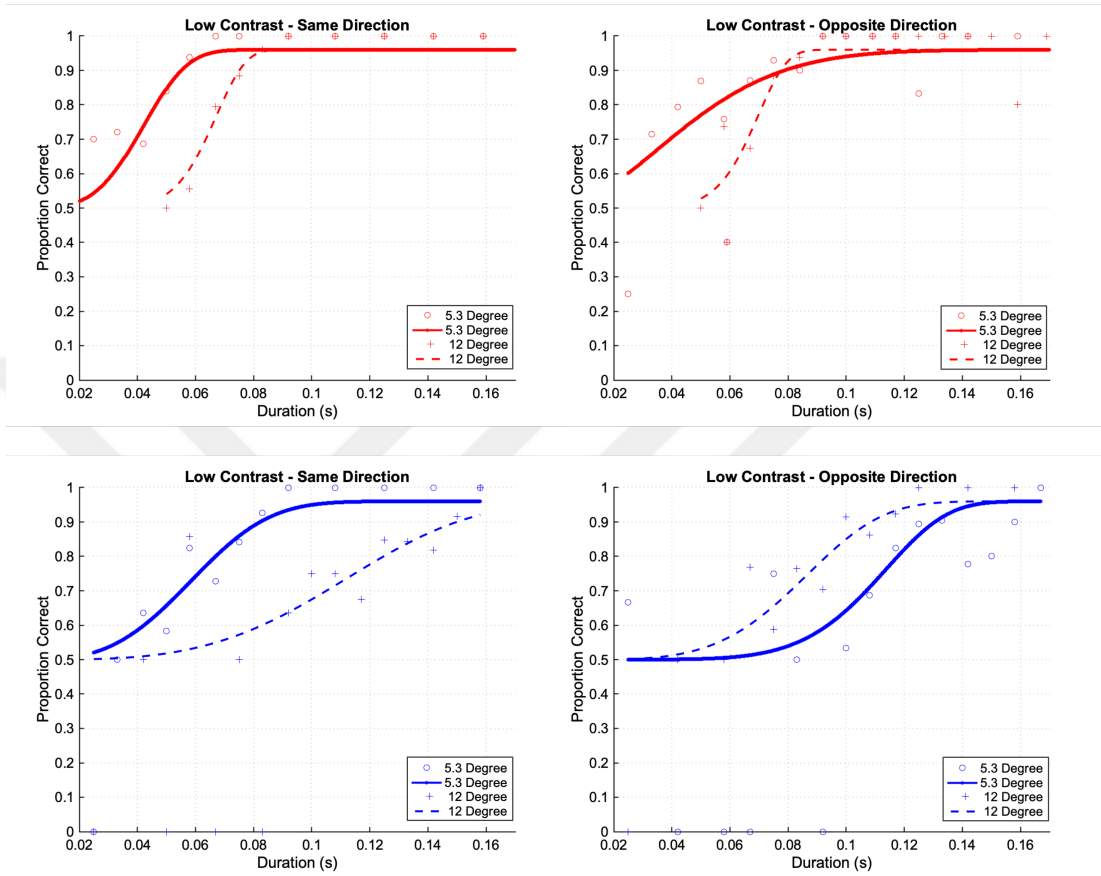


Figure A.9: Weibull function fits for a single participant (3) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

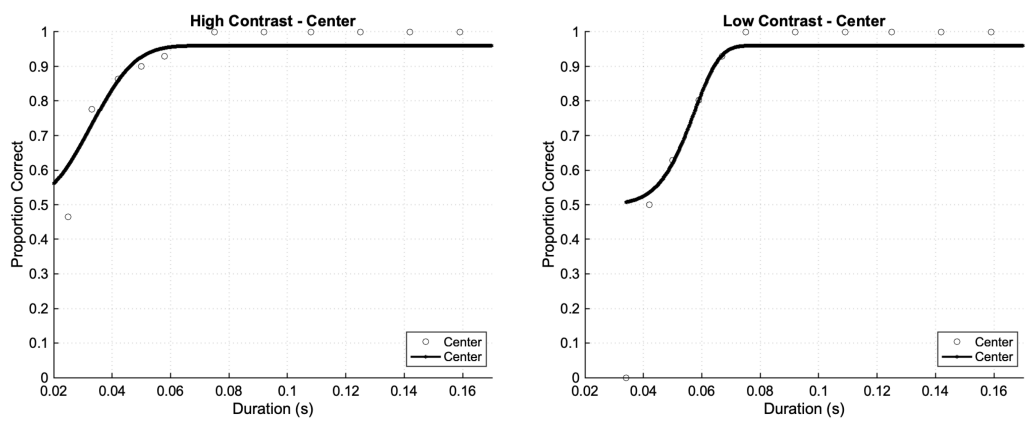


Figure A.10: Weibull function fits for a single participant (4) for center-only condition.

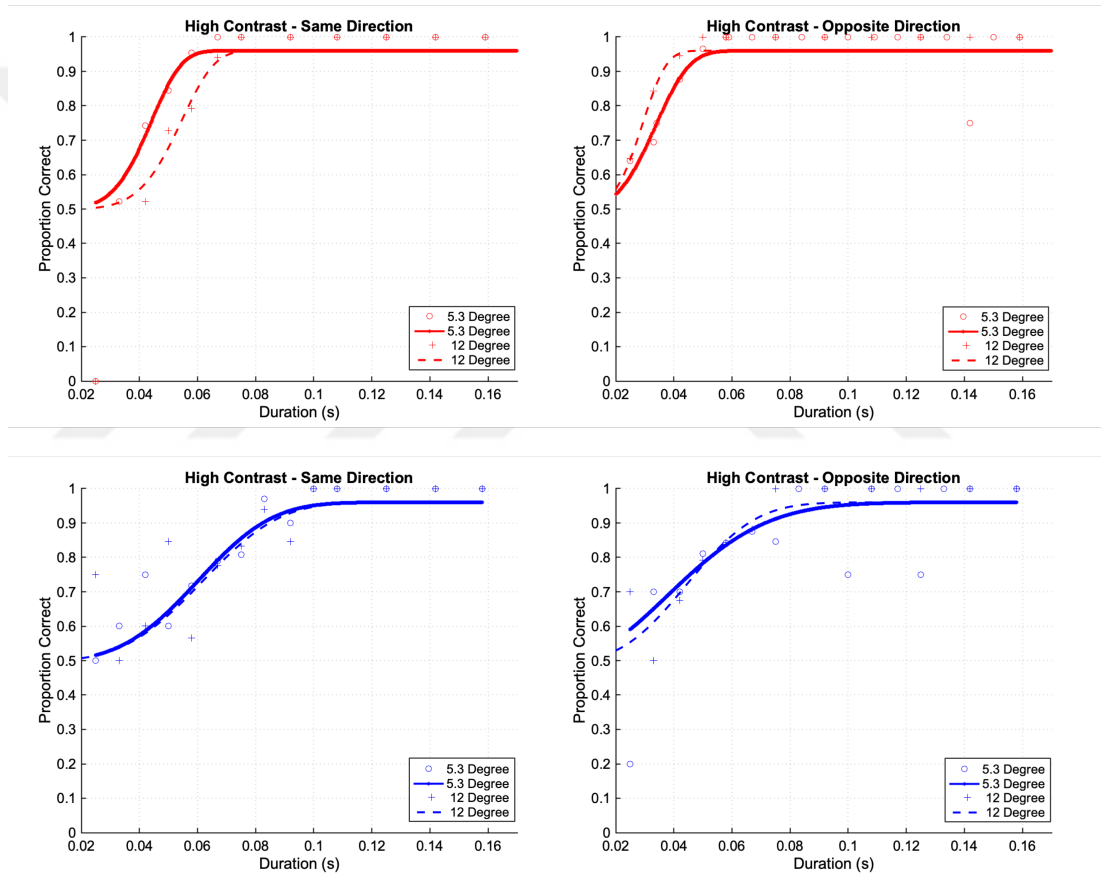


Figure A.11: Weibull function fits for a single participant (4) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

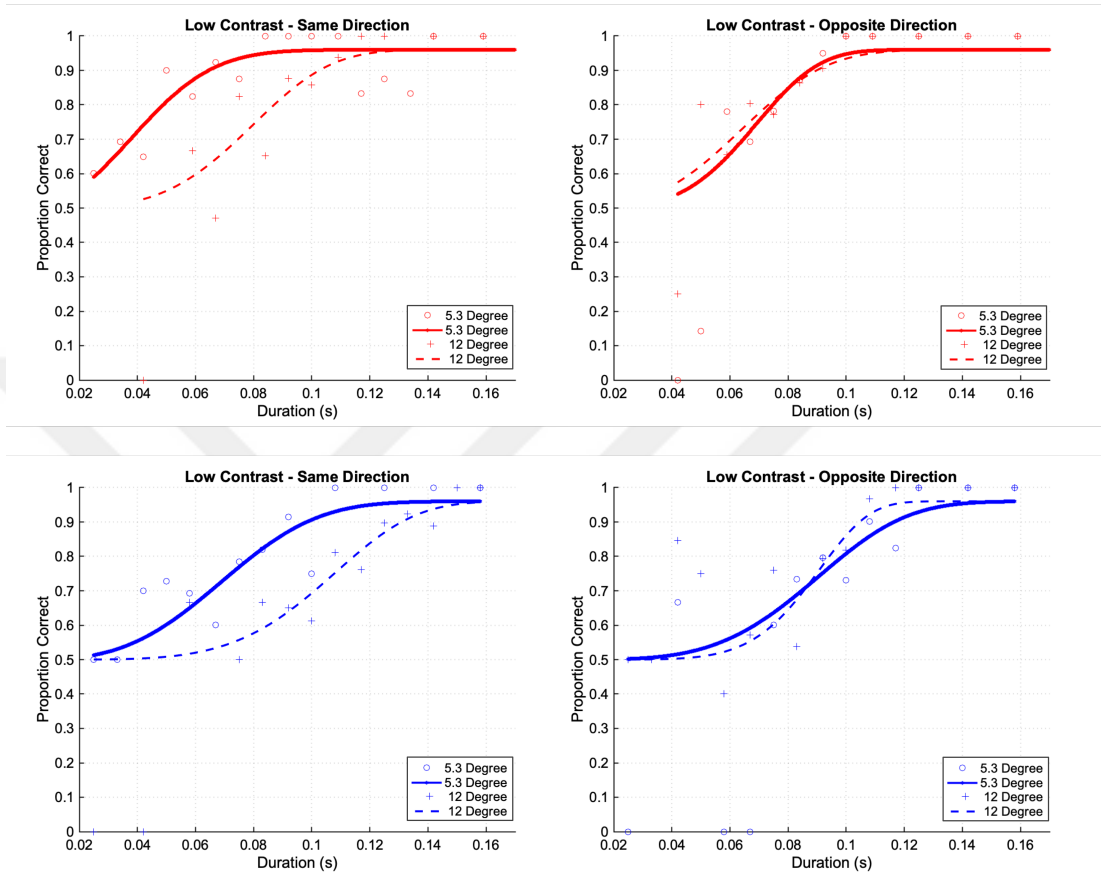


Figure A.12: Weibull function fits for a single participant (4) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

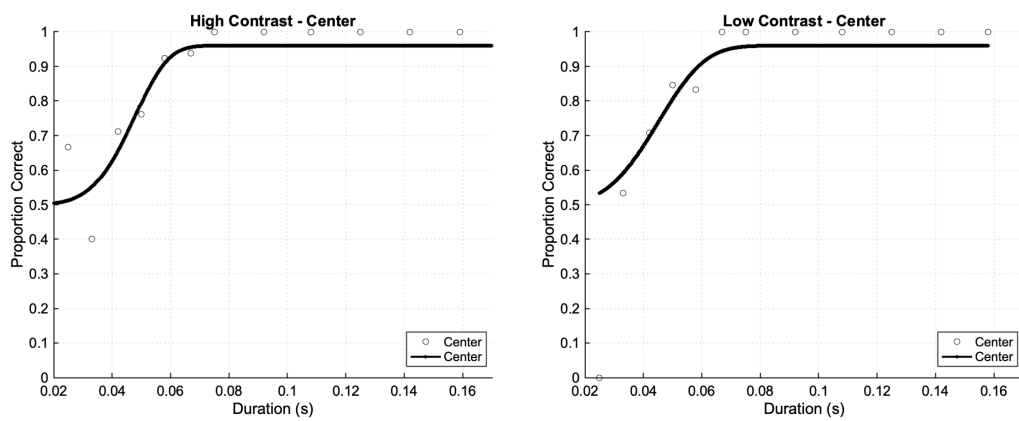


Figure A.13: Weibull function fits for a single participant (5) for center-only condition.

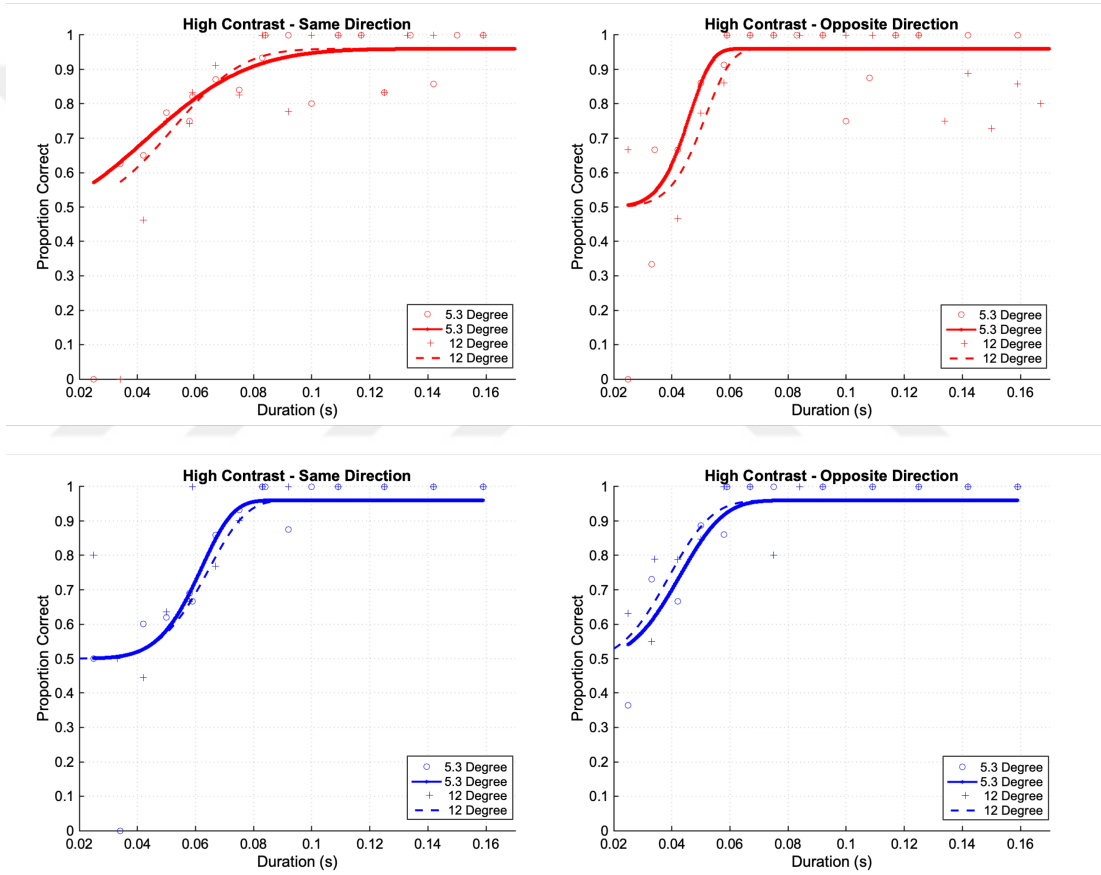


Figure A.14: Weibull function fits for a single participant (5) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

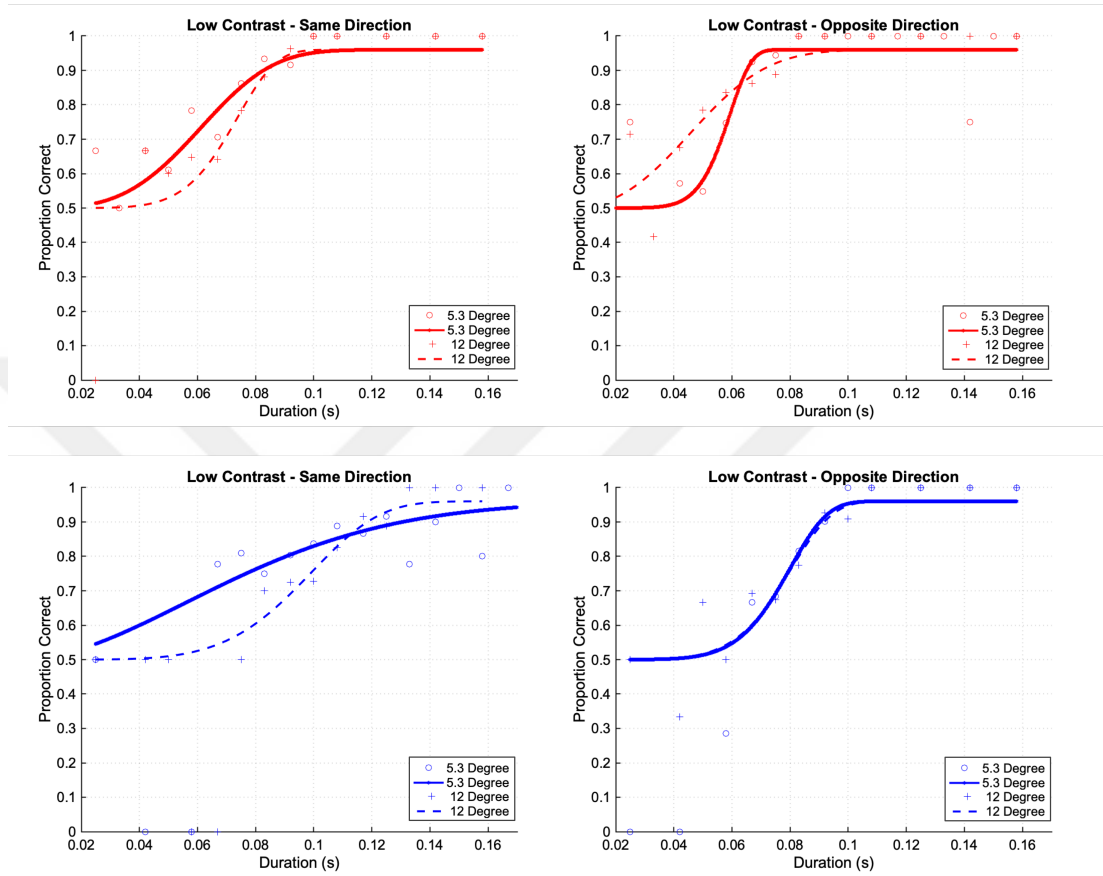


Figure A.15: Weibull function fits for a single participant (5) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

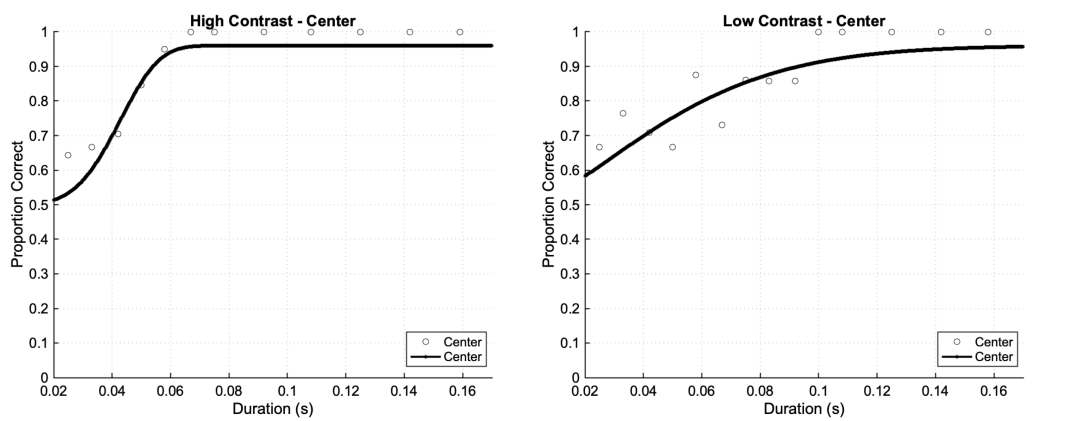


Figure A.16: Weibull function fits for a single participant (6) for center-only condition.

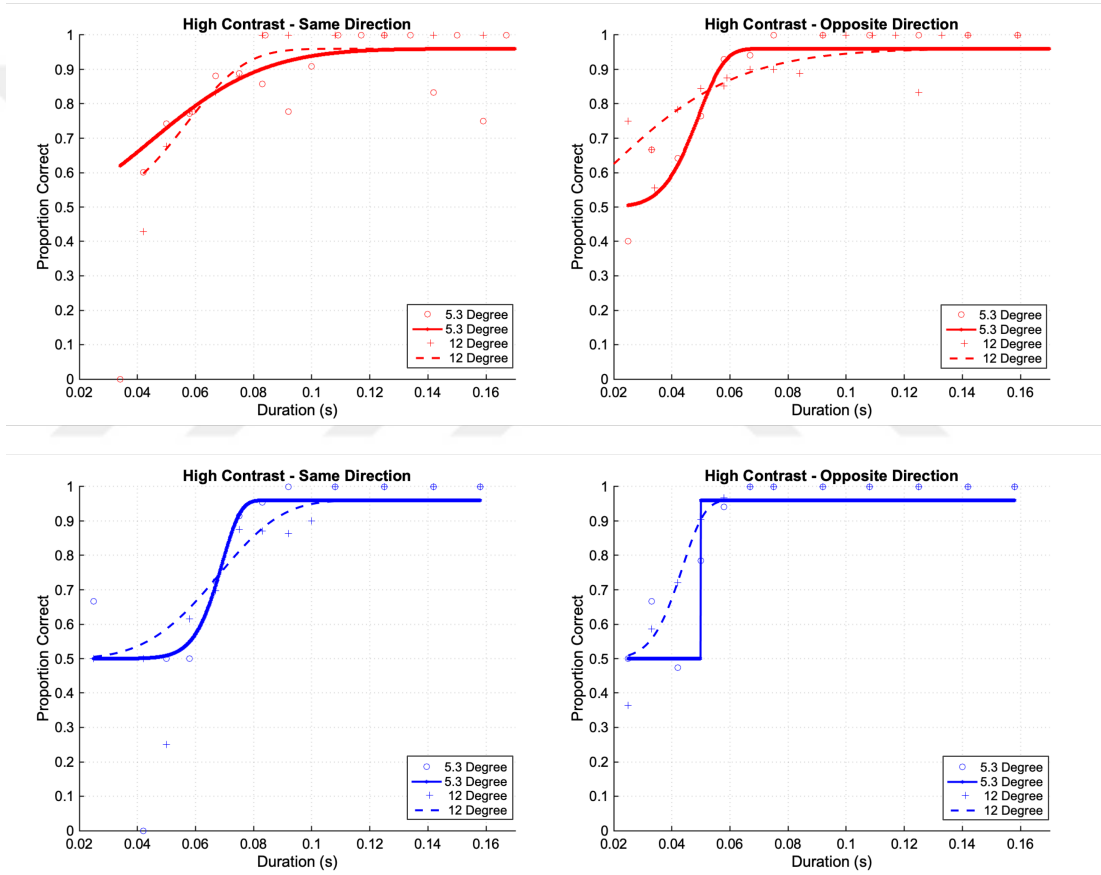


Figure A.17: Weibull function fits for a single participant (6) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

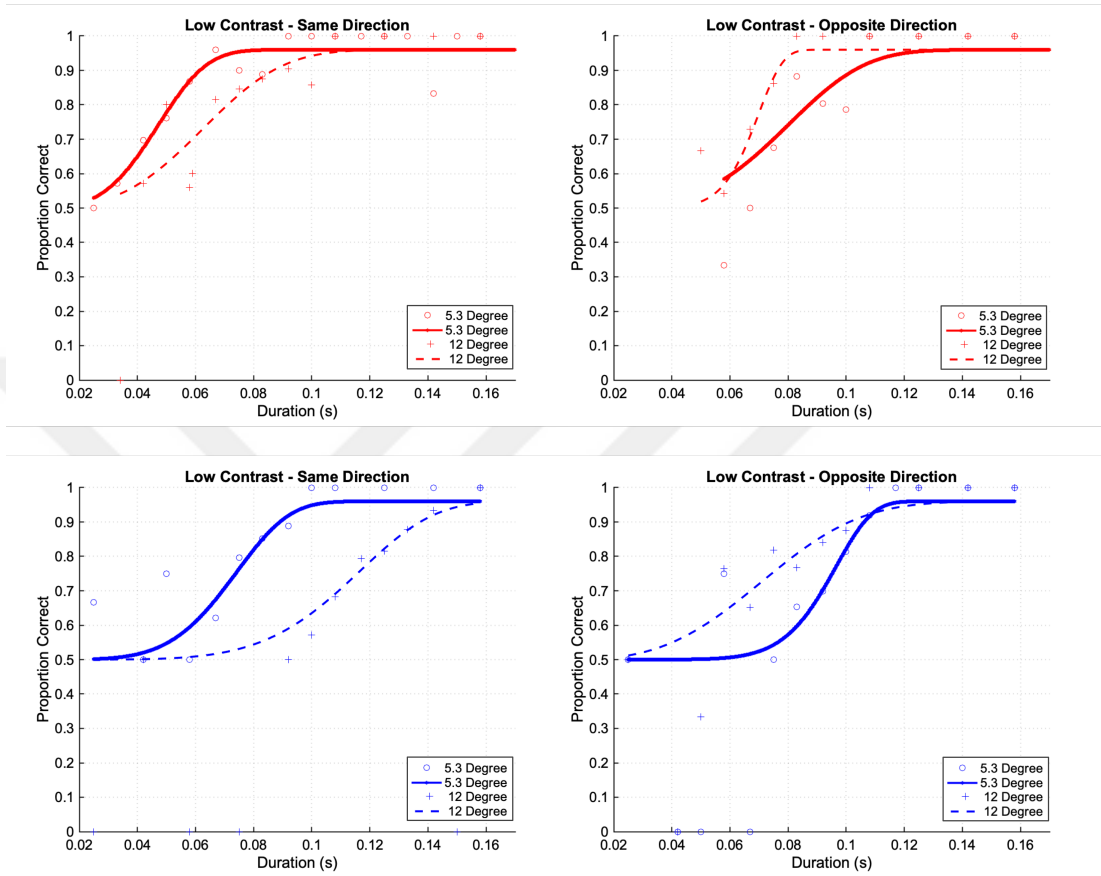


Figure A.18: Weibull function fits for a single participant (6) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

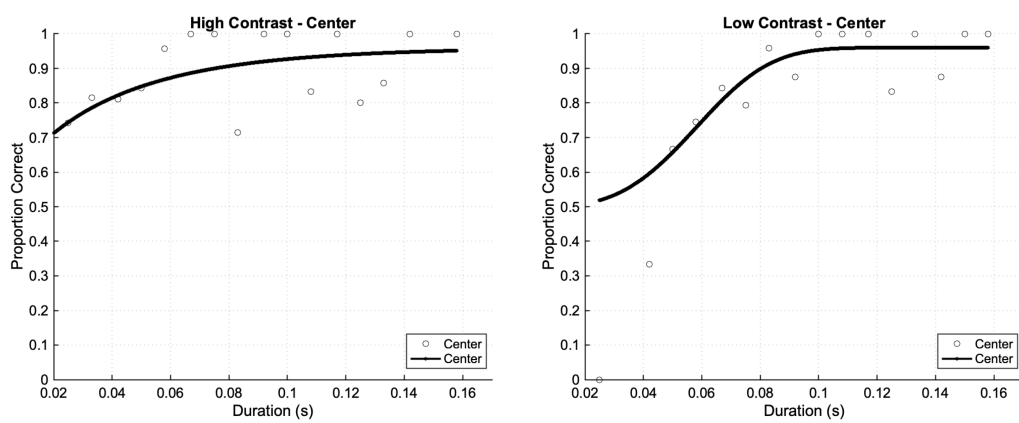


Figure A.19: Weibull function fits for a single participant (7) for center-only condition.

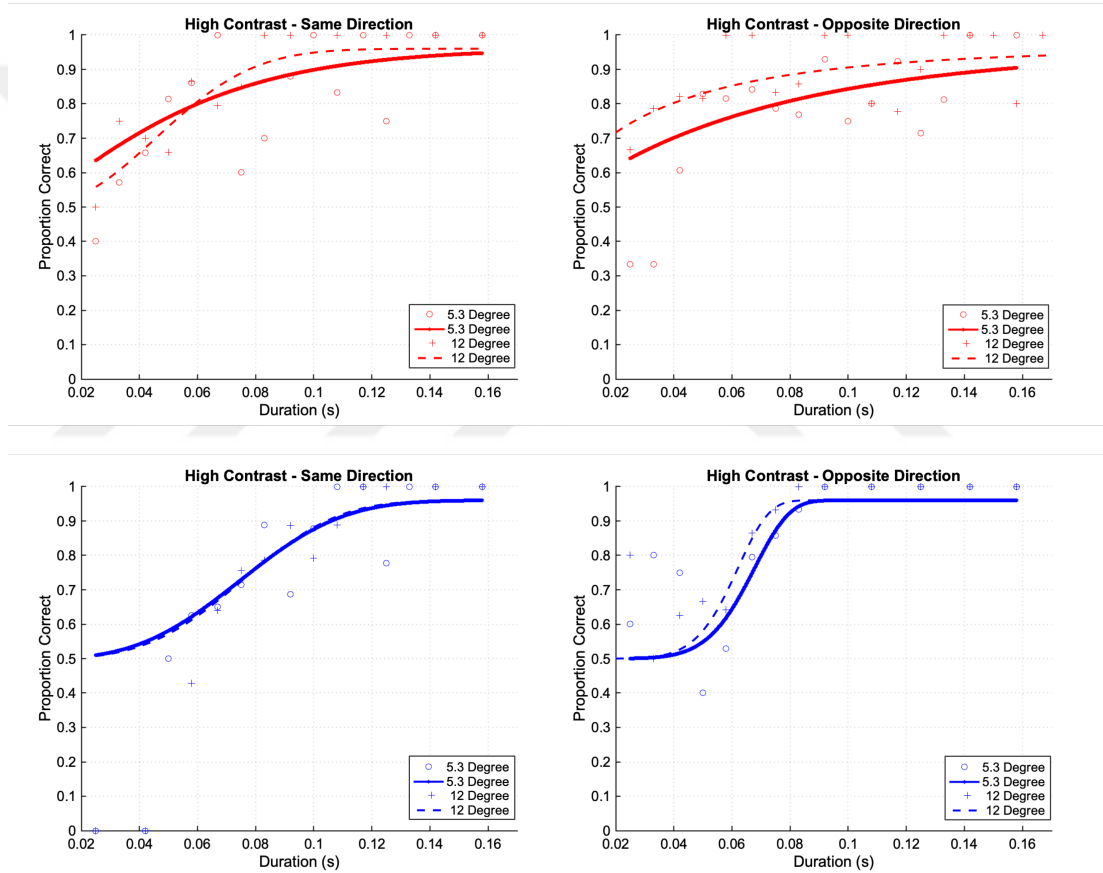


Figure A.20: Weibull function fits for a single participant (7) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

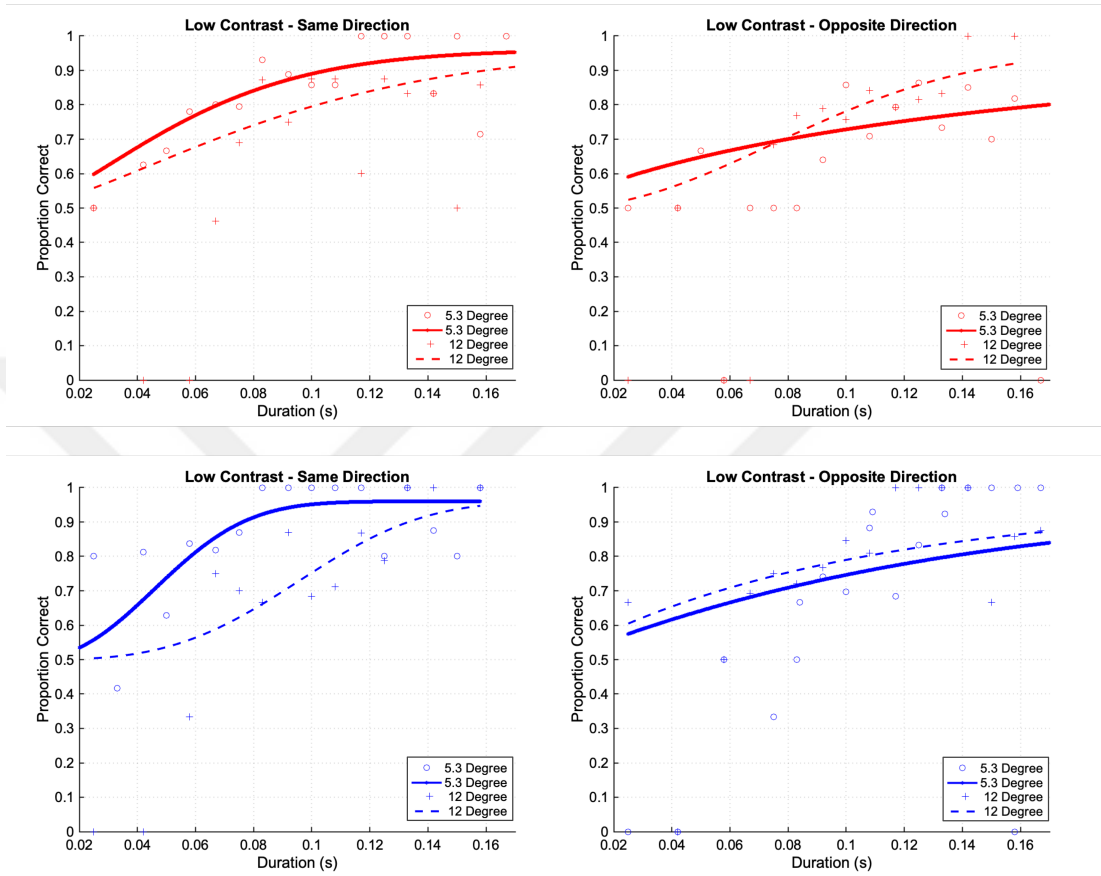


Figure A.21: Weibull function fits for a single participant (7) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

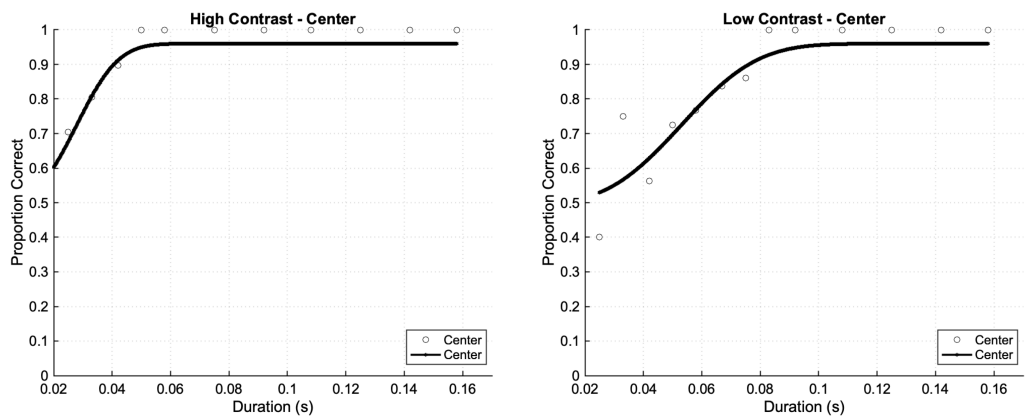


Figure A.22: Weibull function fits for a single participant (8) for center-only condition.

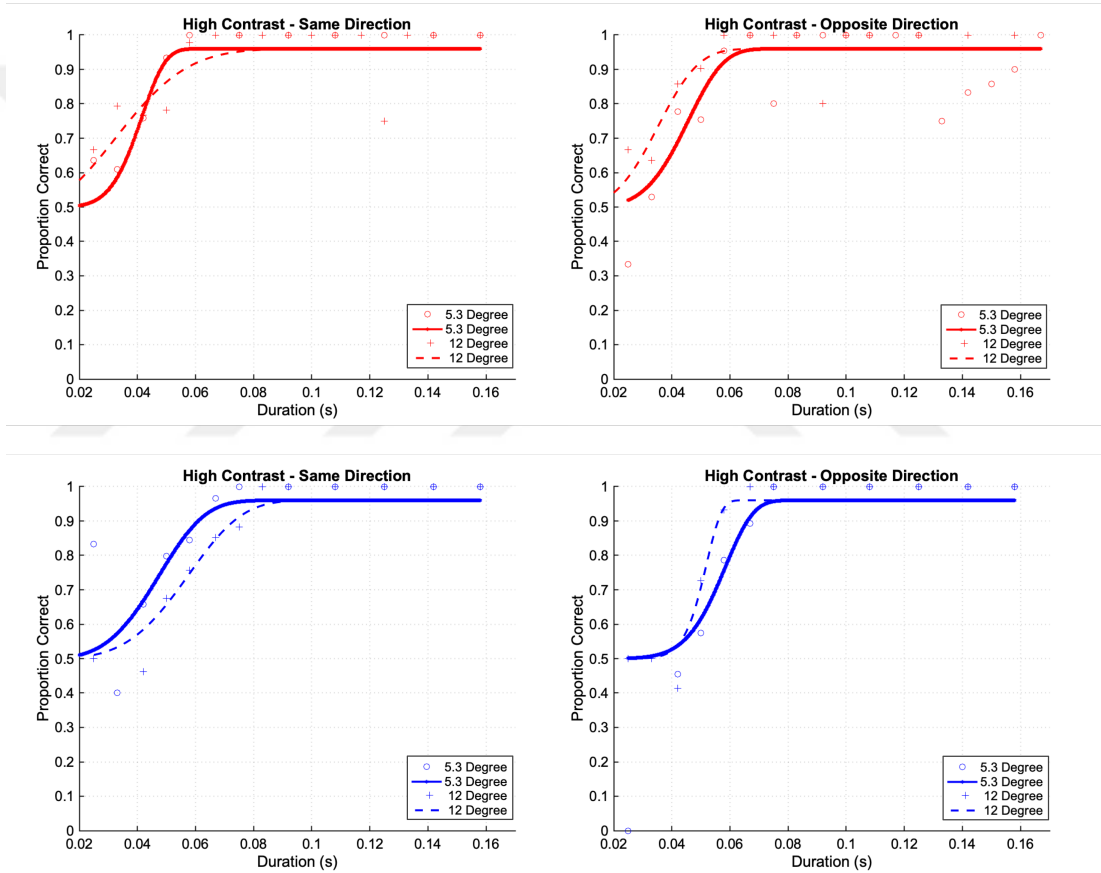


Figure A.23: Weibull function fits for a single participant (8) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

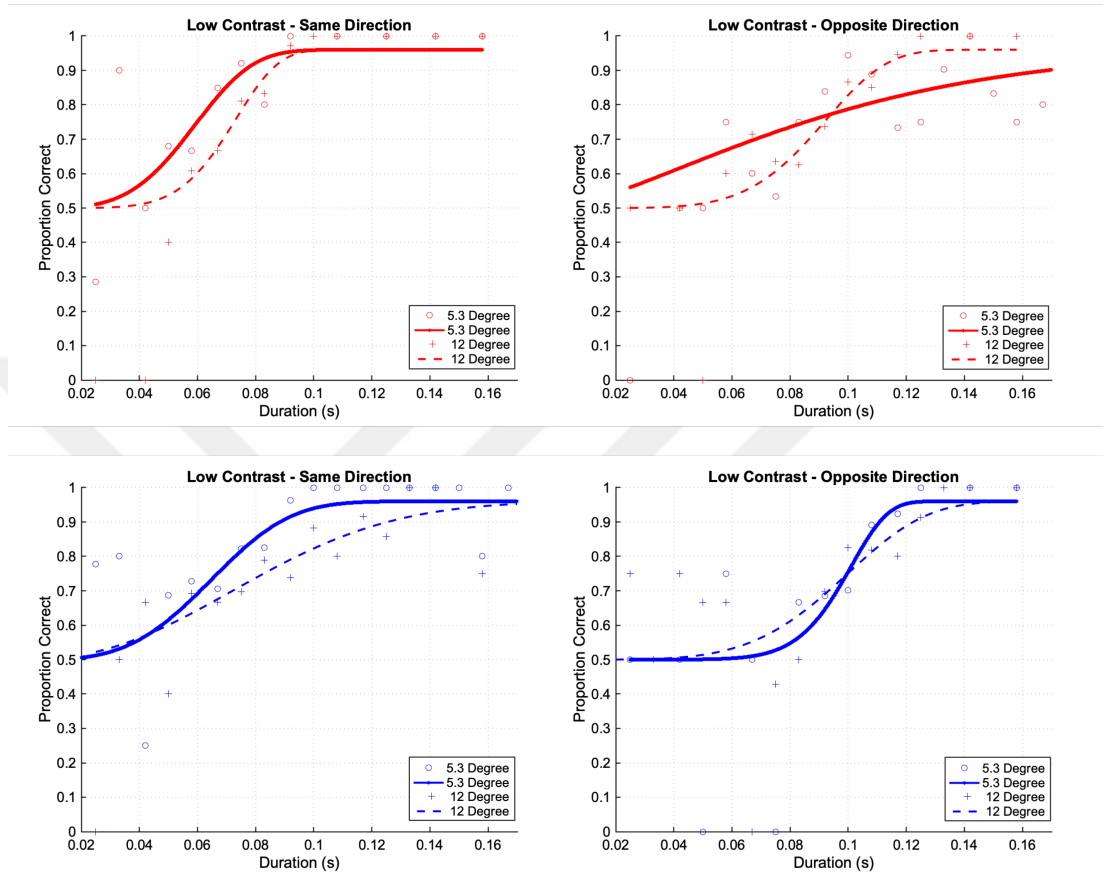


Figure A.24: Weibull function fits for a single participant (8) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

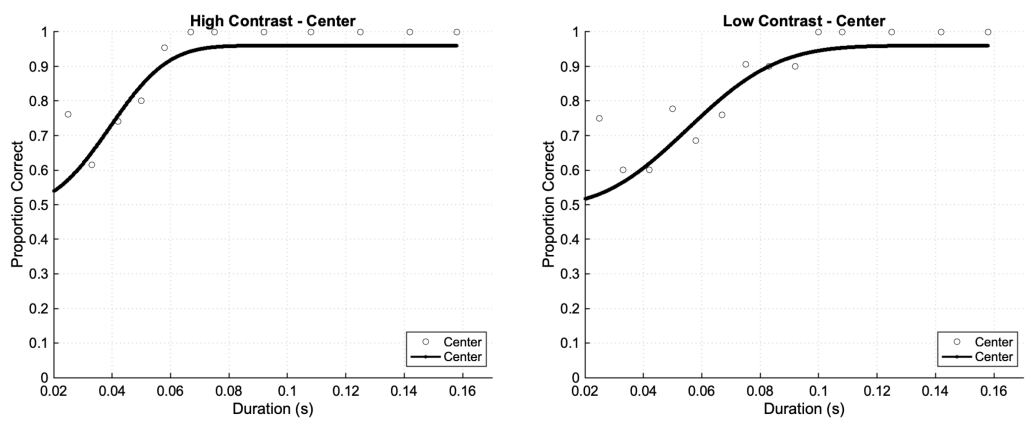


Figure A.25: Weibull function fits for a single participant (9) for center-only condition.

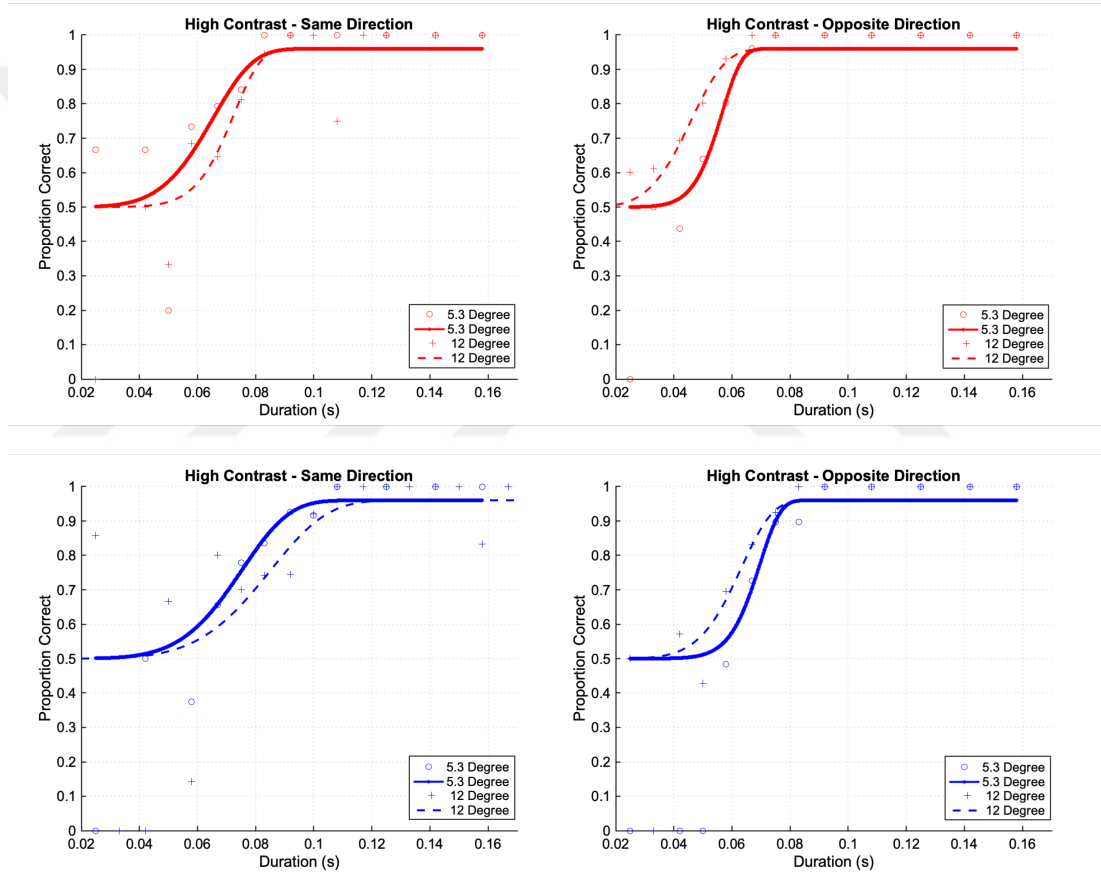


Figure A.26: Weibull function fits for a single participant (9) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

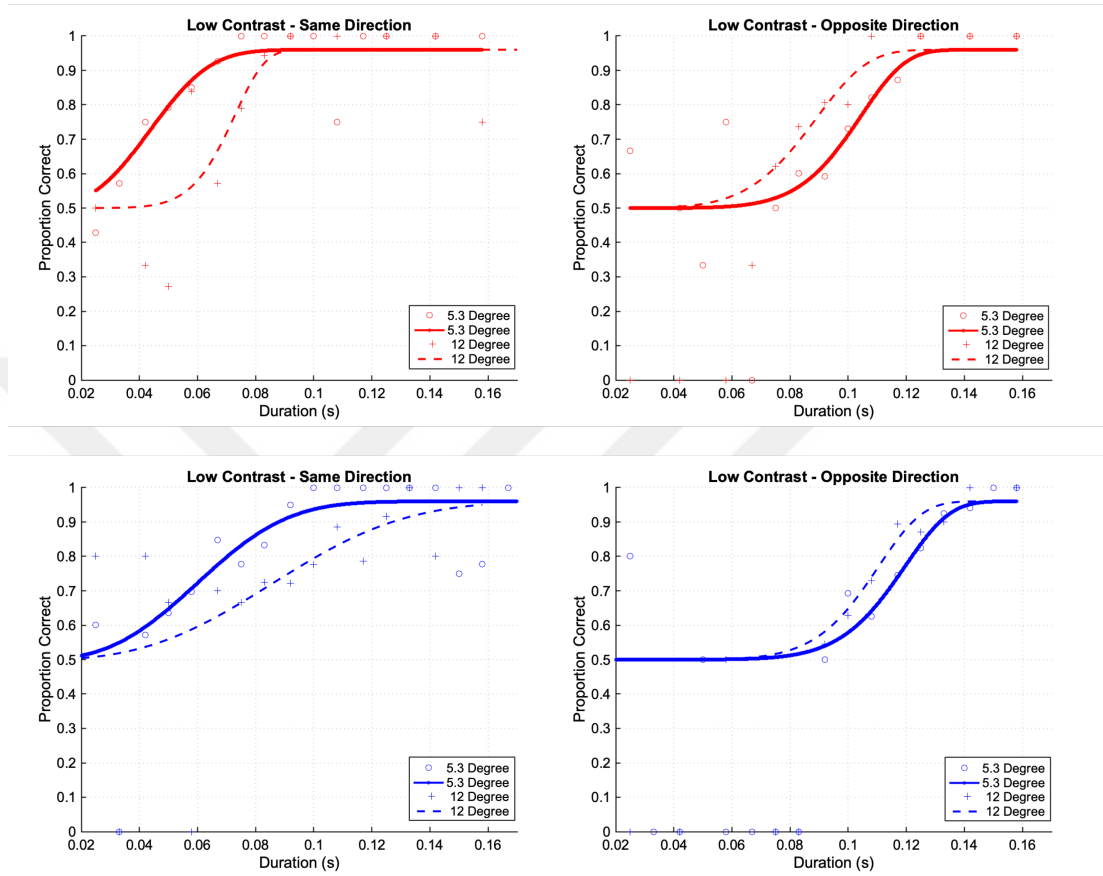


Figure A.27: Weibull function fits for a single participant (9) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

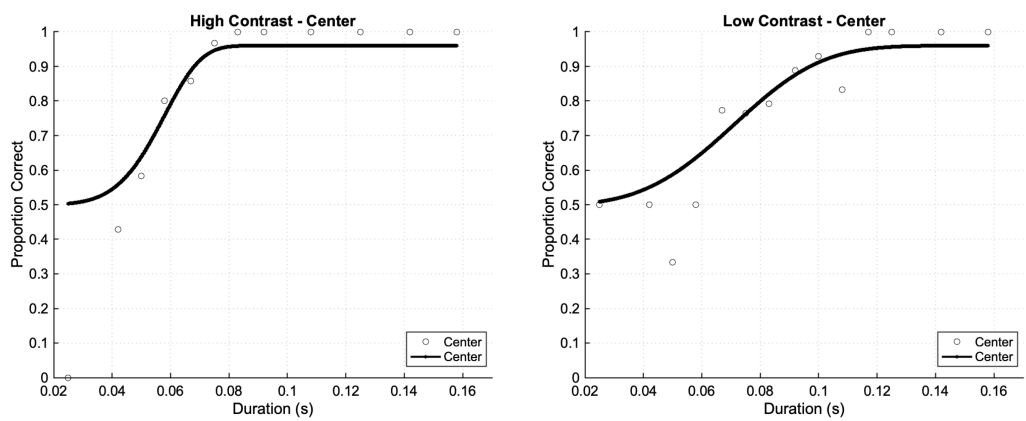


Figure A.28: Weibull function fits for a single participant (10) for center-only condition.

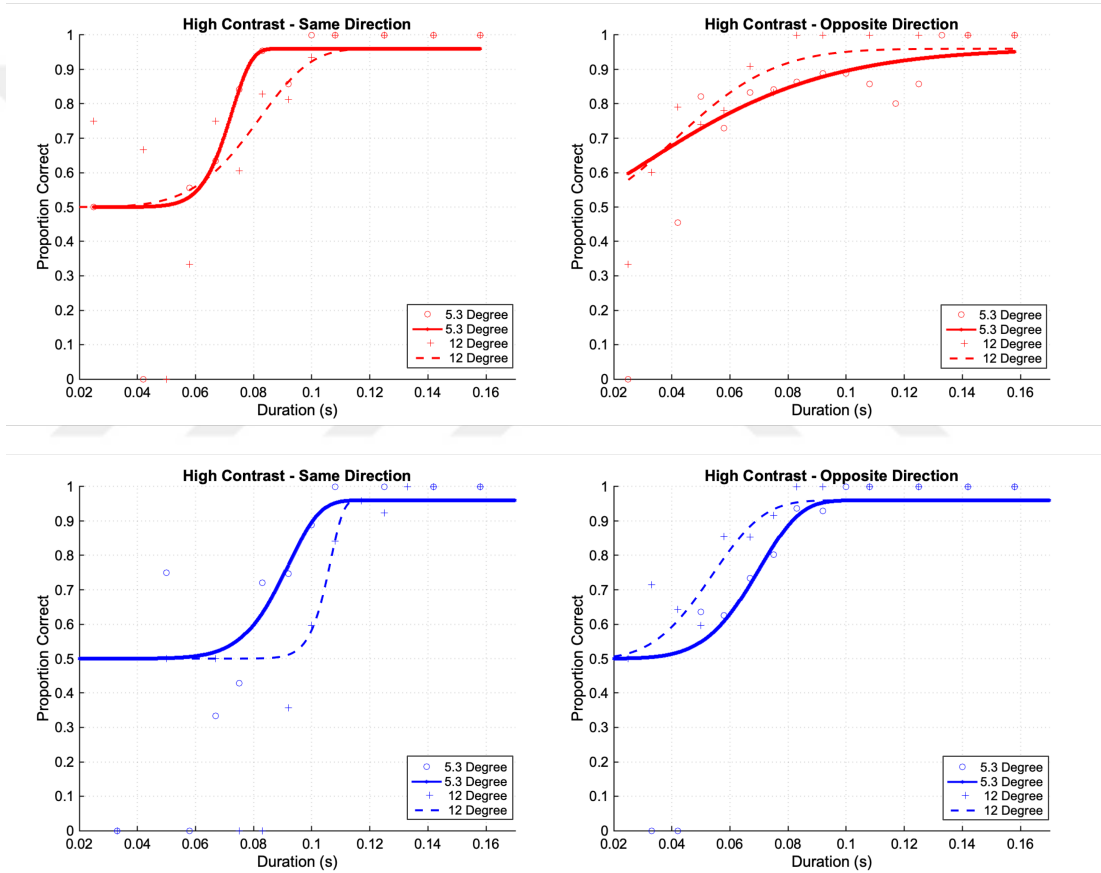


Figure A.29: Weibull function fits for a single participant (10) for high-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

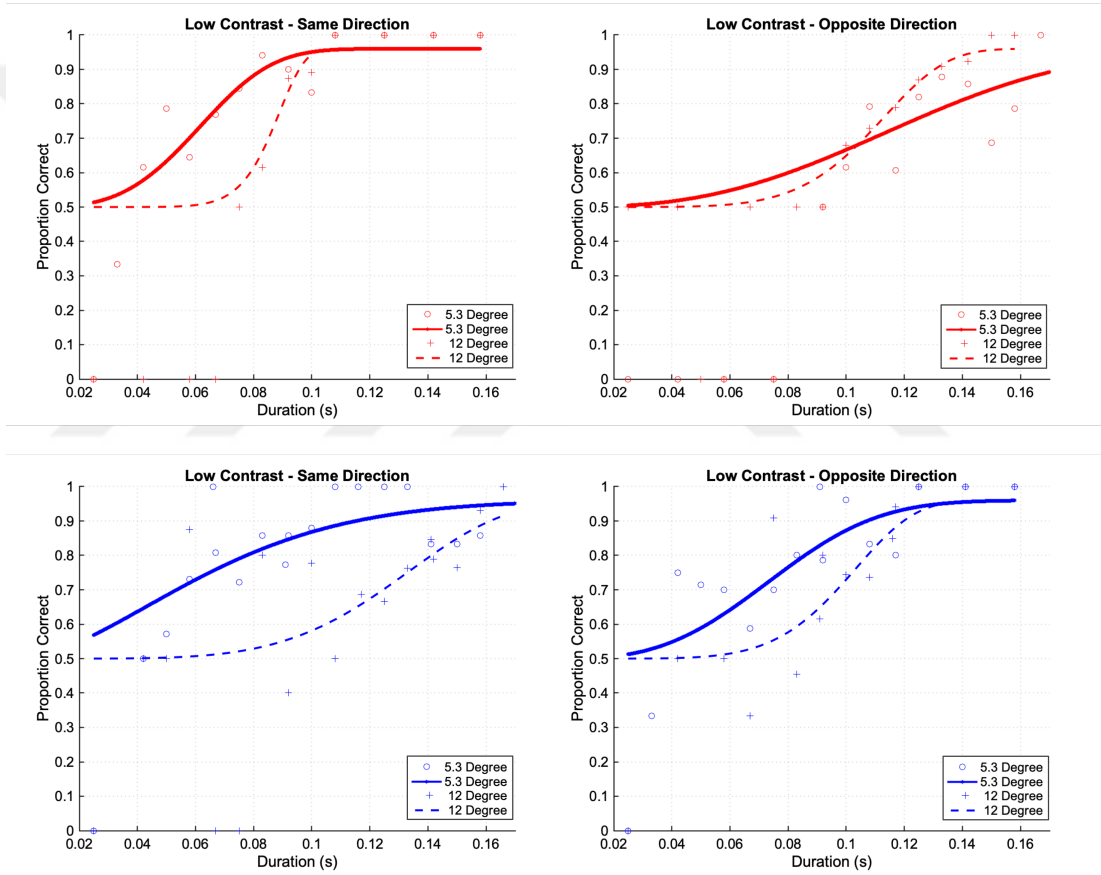


Figure A.30: Weibull function fits for a single participant (10) for low-contrast small-surround and large-surround conditions. First row: Weibull function fits for narrow attention condition. Second row: Weibull function fits for wide attention condition.

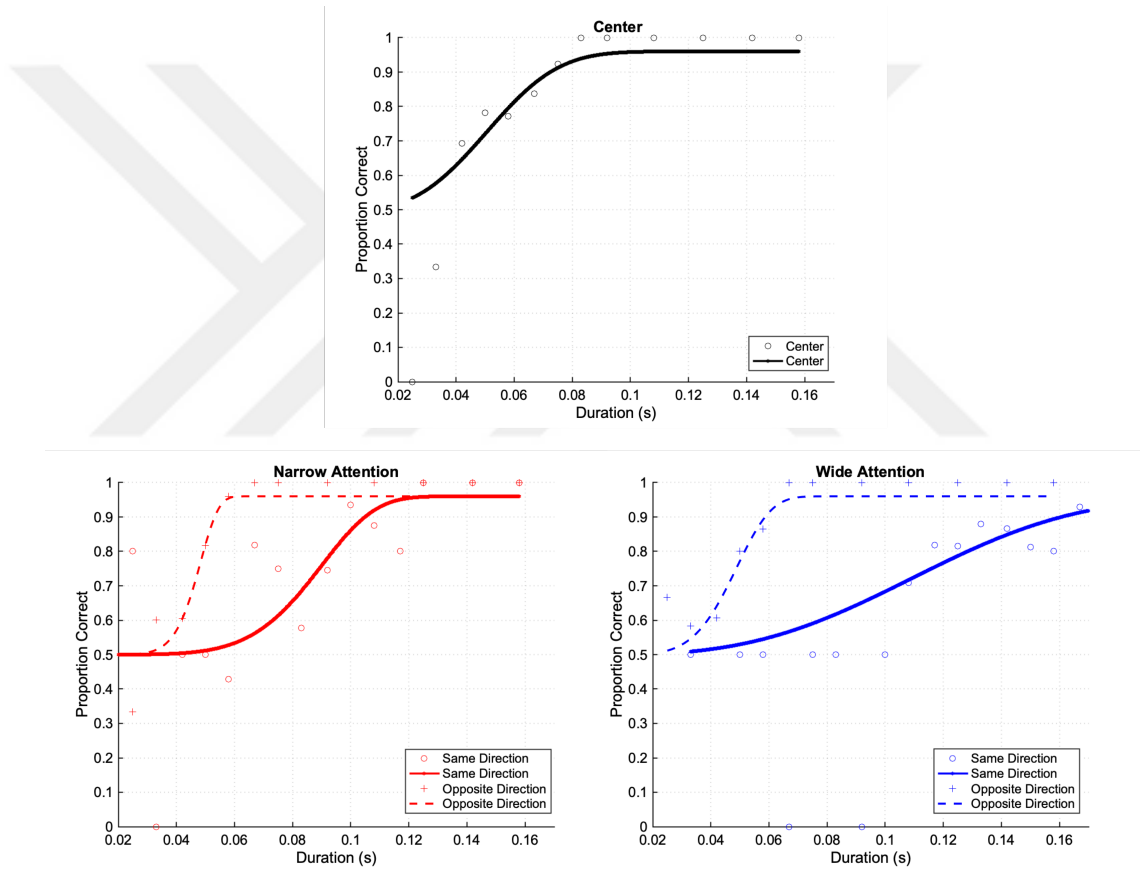


Figure A.31: Weibull function fits for a single participant (1) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.

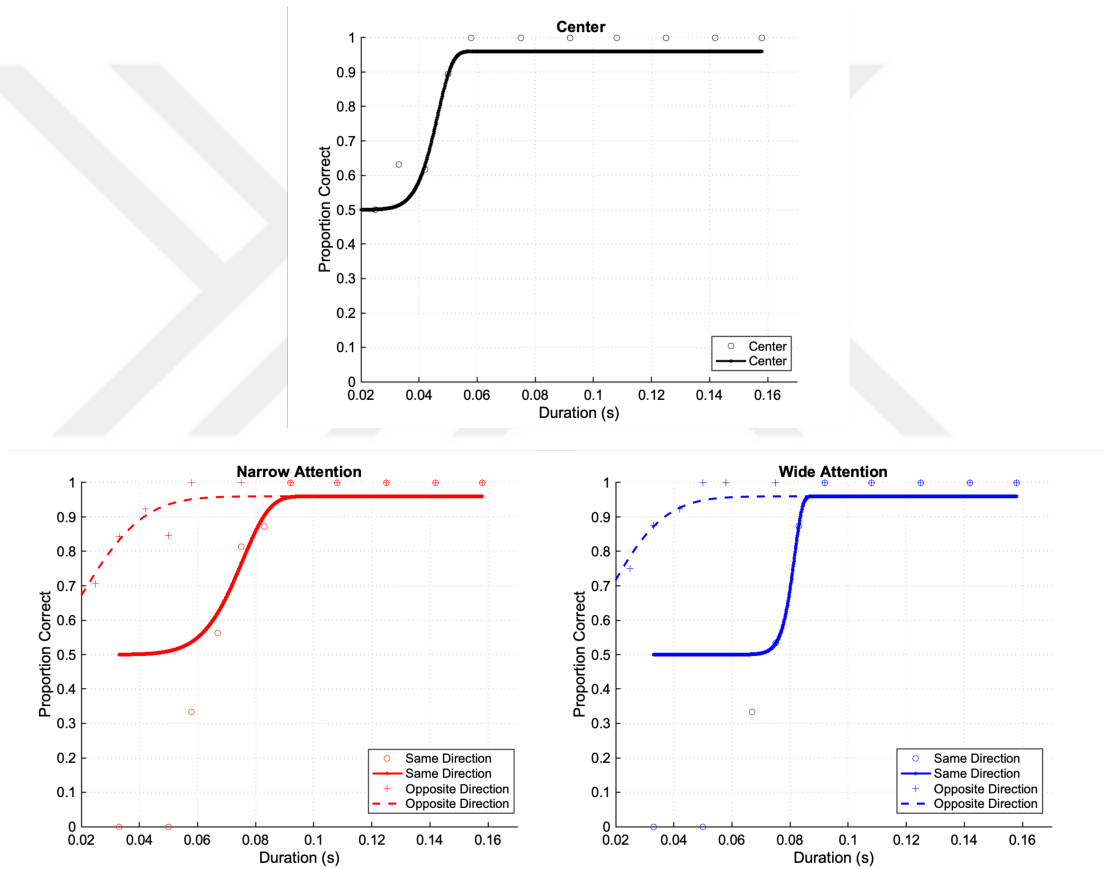


Figure A.32: Weibull function fits for a single participant (2) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.

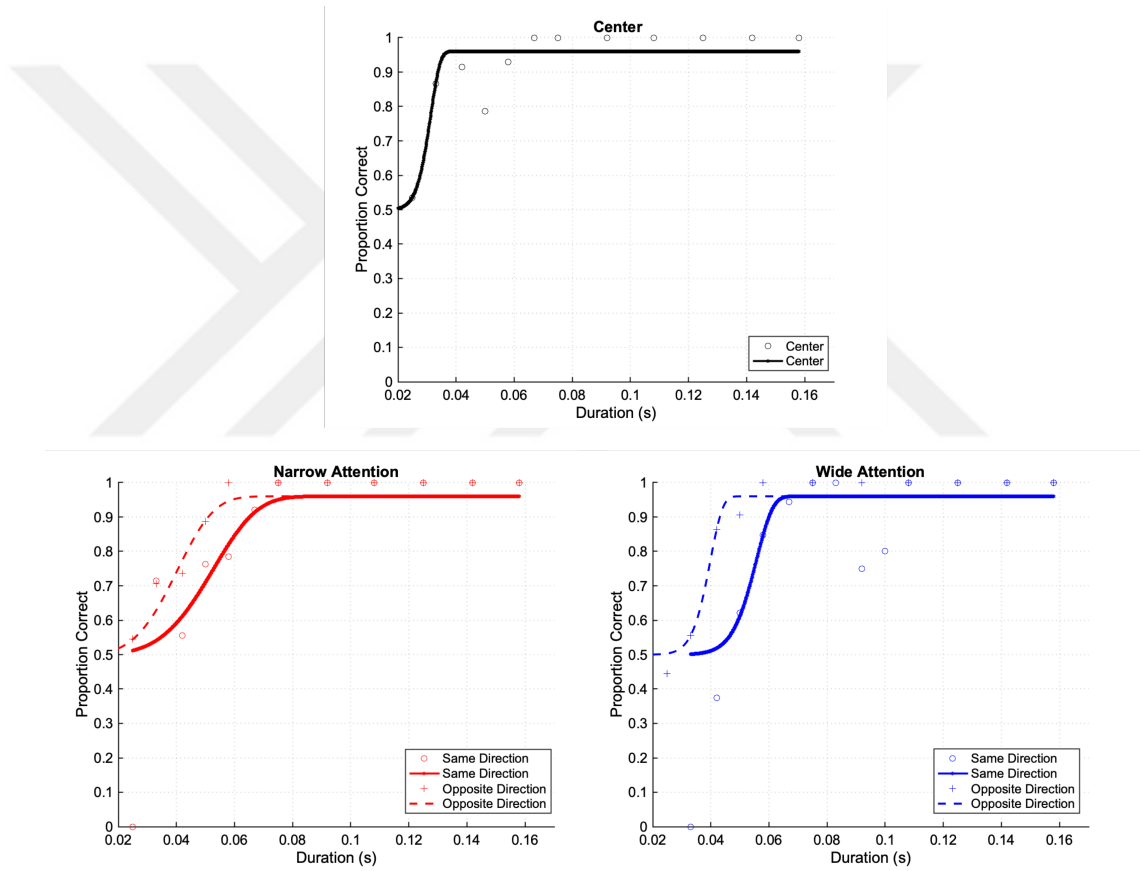


Figure A.33: Weibull function fits for a single participant (3) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.

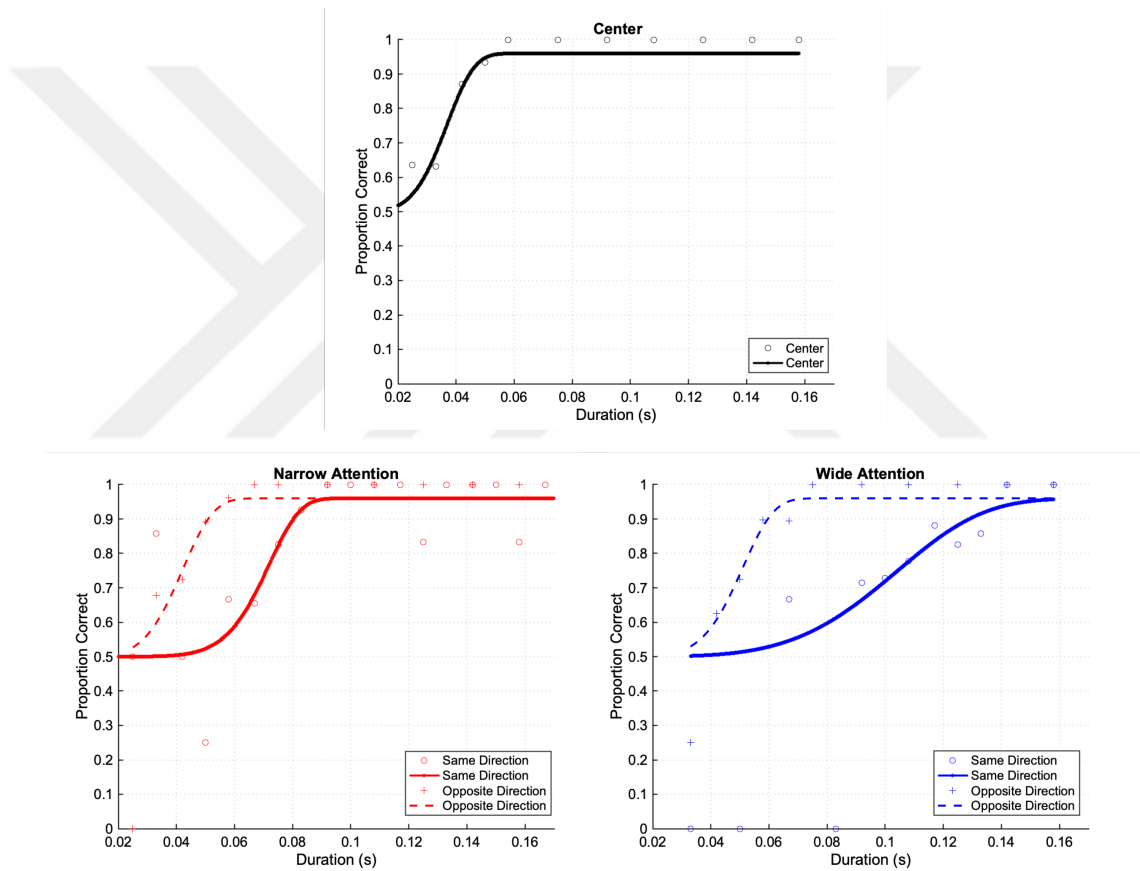


Figure A.34: Weibull function fits for a single participant (4) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.

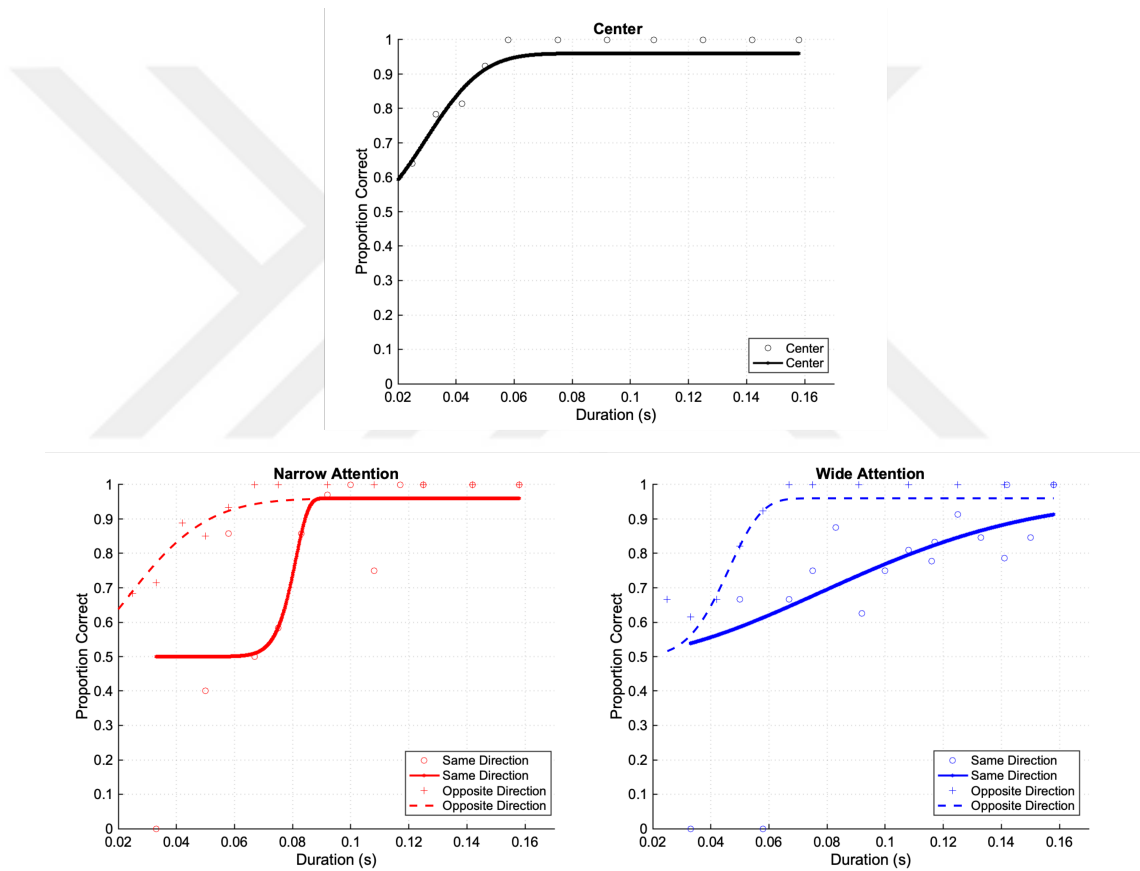


Figure A.35: Weibull function fits for a single participant (5) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.

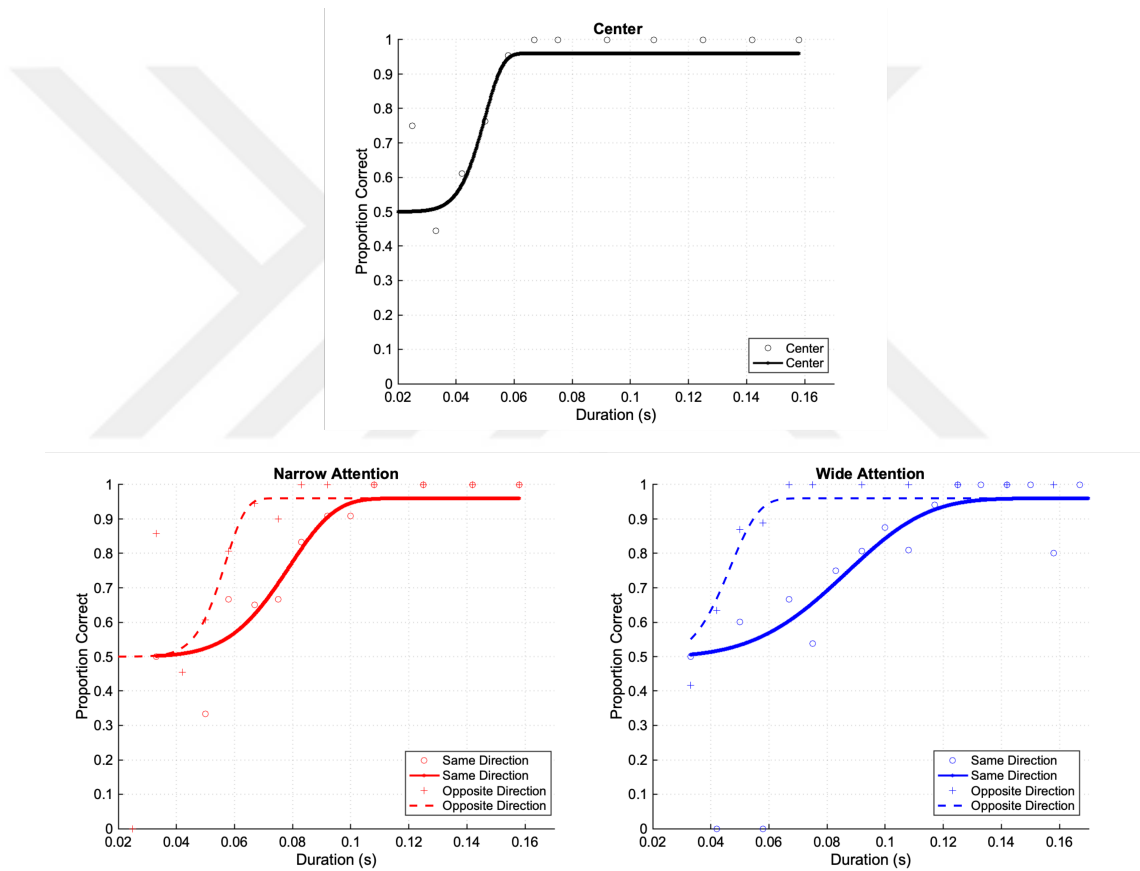


Figure A.36: Weibull function fits for a single participant (6) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.

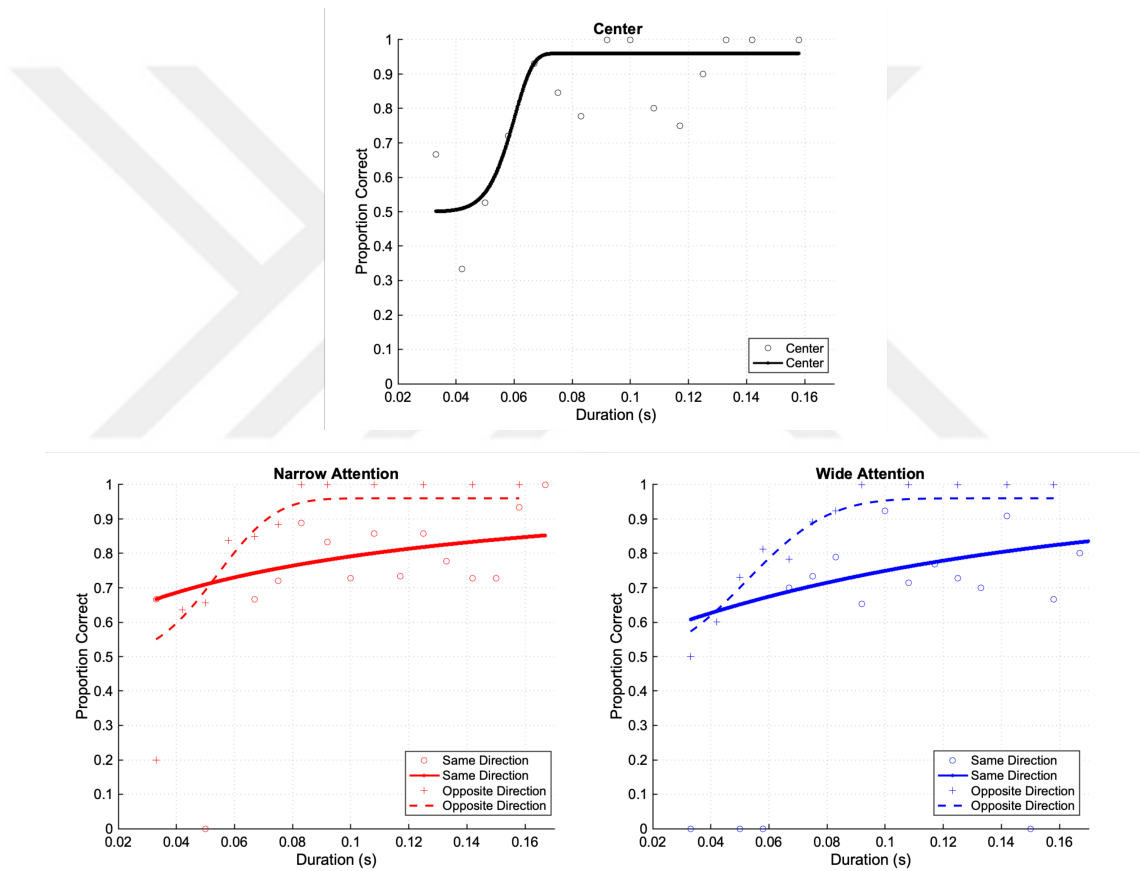


Figure A.37: Weibull function fits for a single participant (7) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.

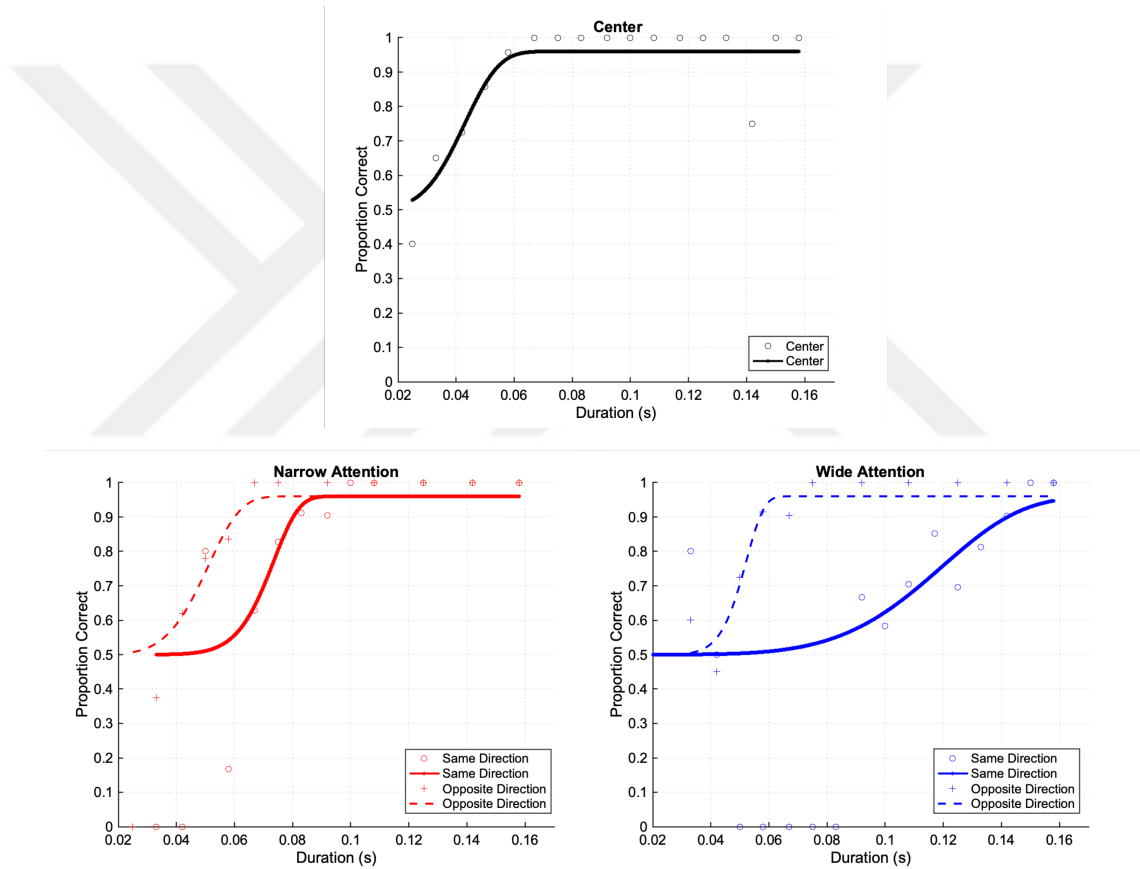


Figure A.38: Weibull function fits for a single participant (8) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.

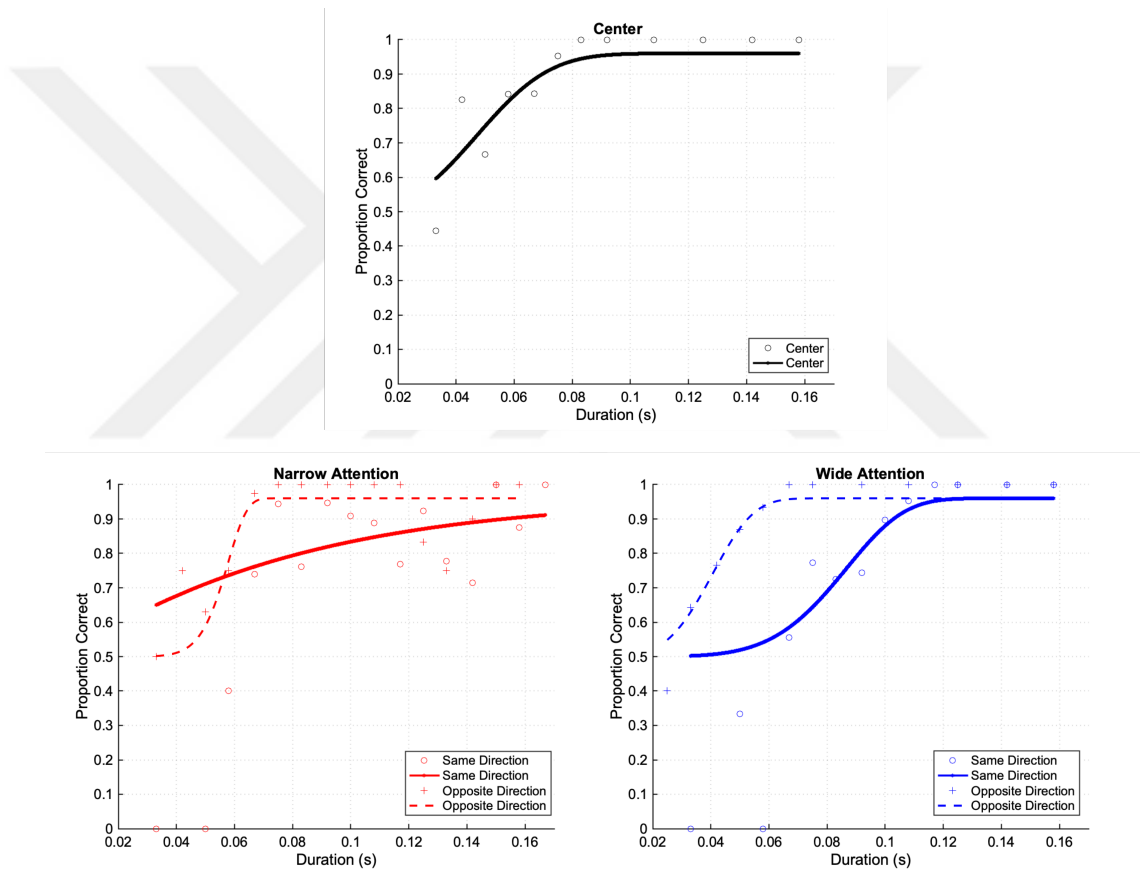


Figure A.39: Weibull function fits for a single participant (9) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.

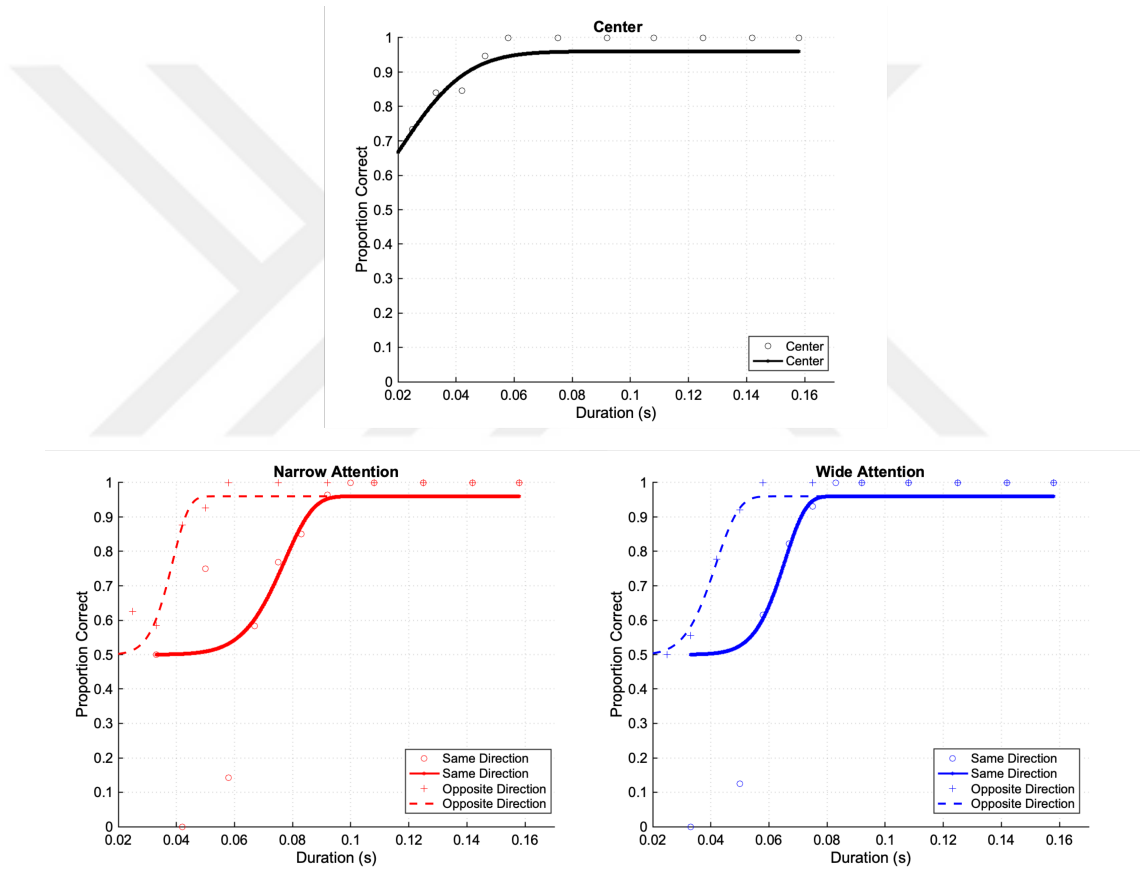


Figure A.40: Weibull function fits for a single participant (10) for center-only, same-direction and opposite-direction conditions. Left: Weibull function fits for narrow attention condition. Right: Weibull function fits for wide attention condition.

Appendix B

Permissions to Re-use Figures



Order Number: 1388678

Order Date: 22 Aug 2023

Payment Information

Merve Kiniklioğlu
mervekiniklioglu@gmail.com
Payment method: Invoice

Billing Address:
Merve Kiniklioğlu
Bilkent University Aysel Sabuncu Brain Research
Center
Ankara, 06800
Turkey

+90 (506)6389525
mervekiniklioglu@gmail.com

Customer Location:
Merve Kiniklioğlu
Bilkent University Aysel Sabuncu Brain Research
Center
Ankara, 06800
Turkey

Order Details

1. Annual Review of Vision Science

Billing Status:
Open

Article: Contributions of Retinal Ganglion Cells to Subcortical Visual Processing and Behaviors.

Order License ID	1388678-1	Type of Use	Republish in a thesis/dissertation
Order detail status	Completed	Publisher	Annual Reviews Inc
ISSN	2374-4650	Portion	Chart/graph/table/figure
			0.00 US
			Republication Permission

LICENSED CONTENT

Publication Title	Annual Review of Vision Science	Publication Type	e-Journal
Article Title	Contributions of Retinal Ganglion Cells to Subcortical Visual Processing and Behaviors.	Start Page	291
		End Page	328
Date	01/01/2015	Issue	1
Country	United States of America	Volume	1
Rightsholder	Annual Reviews, Inc.		

REQUEST DETAILS

Portion Type	Chart/graph/table/figure	Distribution	Worldwide
Number of Charts / Graphs / Tables / Figures Requested	1	Translation	Original language of publication
Format (select all that apply)	Print, Electronic	Copies for the Disabled?	No
Who Will Republish the Content?	Academic institution	Minor Editing Privileges?	No
Duration of Use	Life of current and all future editions	Incidental Promotional Use?	No
Lifetime Unit Quantity	Up to 2,000,000	Currency	USD
Rights Requested	Main product		

NEW WORK DETAILS

Title	BEHAVIORAL AND NEURAL INVESTIGATION ON THE EFFECT OF SPATIAL ATTENTION ON SURROUND SUPPRESSION	Institution Name	Bilkent University
		Expected Presentation Date	2023-09-22
Instructor Name	Merve Kiniklioğlu		

ADDITIONAL DETAILS

The Requesting Person/Organization to Appear on the License

Merve Kiniklioğlu

REQUESTED CONTENT DETAILS

Title, Description or Numeric Reference of the Portion(s)	Figure 1. The retina is a layered structure consisting of five neural cell types	Title of the Article/Chapter the Portion Is From	Contributions of Retinal Ganglion Cells to Subcortical Visual Processing and Behaviors.
Editor of Portion(s)	Dhande, Onkar S.; Stafford, Benjamin K.; Lim, Jung-Hwan A.; Huberman, Andrew D.	Author of Portion(s)	Dhande, Onkar S.; Stafford, Benjamin K.; Lim, Jung-Hwan A.; Huberman, Andrew D.
Volume / Edition	1	Issue, if Republishing an Article From a Serial	1
Page or Page Range of Portion	291-328	Publication Date of Portion	2015-11-24

Total Items: 1

 Subtotal: 0.00 US
 Order Total: 0.00 US

Marketplace Permissions General Terms and Conditions

The following terms and conditions ("General Terms"), together with any applicable Publisher Terms and Conditions, govern User's use of Works pursuant to the Licenses granted by Copyright Clearance Center, Inc. ("CCC") on behalf of the applicable Rightsholders of such Works through CCC's applicable Marketplace transactional licensing services (each, "Service").

1) **Definitions.** For purposes of these General Terms, the following definitions apply:

"License" is the licensed use the User obtains via the Marketplace platform in a particular licensing transaction, as set forth in the Order Confirmation.

"Order Confirmation" is the confirmation CCC provides to the User at the conclusion of each Marketplace transaction. "Order Confirmation Terms" are additional terms set forth in specific Order Confirmations not set forth in the General Terms that can include terms applicable to a particular CCC transactional licensing service and/or any Rightsholder-specific terms.

"Rightsholder(s)" are the holders of copyright rights in the Works for which a User obtains licenses via the Marketplace platform, which are displayed on specific Order Confirmations.

"Terms" means the terms and conditions set forth in these General Terms and any additional Order Confirmation Terms collectively.

"User" or "you" is the person or entity making the use granted under the relevant License. Where the person accepting the Terms on behalf of a User is a freelancer or other third party who the User authorized to accept the General Terms on the User's behalf, such person shall be deemed jointly a User for purposes of such Terms.

"Work(s)" are the copyright protected works described in relevant Order Confirmations.

2) **Description of Service.** CCC's Marketplace enables Users to obtain Licenses to use one or more Works in accordance with all relevant Terms. CCC grants Licenses as an agent on behalf of the copyright rightsholder identified in the relevant Order Confirmation.

3) **Applicability of Terms.** The Terms govern User's use of Works in connection with the relevant License. In the event of any conflict between General Terms and Order Confirmation Terms, the latter shall govern. User acknowledges that Rightsholders have complete discretion whether to grant any permission, and whether to place any limitation on any grant, and that CCC has no right to supersede or to modify any such discretionary act by a Rightsholder.

4) **Representations; Acceptance.** By using the Service, User represents and warrants that User has been duly authorized by the User to accept, and hereby does accept, all Terms

5) **Scope of License; Limitations and Obligations.** All Works and all rights therein, including copyright rights, remain the sole and exclusive property of the Rightsholder. The License provides only those rights expressly set forth in the terms and conveys no other rights in any Works

6) **General Payment Terms.** User may pay at time of checkout by credit card or choose to be invoiced. If the User chooses to be invoiced, the User shall: (i) remit payments in the manner identified on specific invoices, (ii) unless otherwise specifically stated in an Order Confirmation or separate written agreement, Users shall remit payments upon receipt of the relevant invoice from CCC, either by delivery or notification of availability of the invoice via the Marketplace platform, and (iii) if the User does not pay the invoice within 30 days of receipt, the User may incur a service charge of 1.5% per month or the maximum rate allowed by applicable law, whichever is less. While User may exercise the rights in the License immediately upon receiving the Order Confirmation, the License is automatically revoked and is null and void, as if it had never been issued, if CCC does not receive complete payment on a timely basis.

7) **General Limits on Use.** Unless otherwise provided in the Order Confirmation, any grant of rights to User (i) involves only the rights set forth in the Terms and does not include subsequent or additional uses, (ii) is non-exclusive and non-transferable, and (iii) is subject to any and all limitations and restrictions (such as, but not limited to, limitations on duration of use or circulation) included in the Terms. Upon completion of the licensed use as set forth in the Order Confirmation, User shall either secure a new permission for further use of the Work(s) or immediately cease any new use of the Work(s) and shall render inaccessible (such as by deleting or by removing or severing links or other locators) all further copies of the Work. User may only make alterations to the Work if and as expressly set forth in the Order Confirmation. No Work may be used in any way that is unlawful, including without limitation if such use would violate applicable sanctions laws or regulations, would be defamatory, violate the rights of third parties (including such third parties' rights of copyright, privacy, publicity, or other tangible or intangible property), or is otherwise illegal, sexually explicit, or obscene. In addition, User may not conjoin a Work with any other material that may result in damage to the reputation of the Rightsholder. Any unlawful use will render any licenses hereunder null and void. User agrees to inform CCC if becomes aware of any infringement of any rights in a Work and to cooperate with any reasonable request of CCC or the Rightsholder in connection therewith.

8) **Third Party Materials.** In the event that the material for which a License is sought includes third party materials (such as photographs, illustrations, graphs, inserts and similar materials) that are identified in such material as having been used by permission (or a similar indicator), User is responsible for identifying, and seeking separate licenses (under this Service, if available, or otherwise) for any of such third party materials; without a separate license, User may not use such third party materials via the License.

9) **Copyright Notice.** Use of proper copyright notice for a Work is required as a condition of any License granted under the Service. Unless otherwise provided in the Order Confirmation, a proper copyright notice will read substantially as follows: "Used with permission of [Rightsholder's name], from [Work's title, author, volume, edition number and year of copyright]; permission conveyed through Copyright Clearance Center, Inc." Such notice must be provided in a reasonably legible font size and must be placed either on cover page or in another location that any person, upon gaining access to the material which is the subject of a permission, shall see, or in the case of republication License immediately adjacent to the Work as used (for example, as part of a by-line or footnote) or in the place where substantially all other credits or notices for the new work containing the republished Work are located. Failure to include the required notice results in loss to the Rightsholder and CCC, and the User shall be liable to pay liquidated damages for each such failure equal to twice the use fee specified in the Order Confirmation, in addition to the use fee itself and any other fees and charges specified.

10) **Indemnity.** User hereby indemnifies and agrees to defend the Rightsholder and CCC, and their respective employees and directors, against all claims, liability, damages, cost and expenses, including legal fees and expenses, arising out of any use of a Work beyond the scope of the rights granted herein and in the Order Confirmation, or any use of Work which has been altered in any unauthorized way by User, including claims of defamation or infringement of rights of copyright, publicity, privacy, or other tangible or intangible property.

11) **Limitation of Liability.** UNDER NO CIRCUMSTANCES WILL CCC OR THE RIGHTSHOLDER BE LIABLE FOR ANY DIRECT, INDIRECT, CONSEQUENTIAL, OR INCIDENTAL DAMAGES (INCLUDING WITHOUT LIMITATION DAMAGES FOR LOSS OF BUSINESS PROFITS OR INFORMATION, OR FOR BUSINESS INTERRUPTION) ARISING OUT OF THE USE OR INABILITY TO USE A WORK, EVEN IF ONE OR BOTH OF THEM HAS BEEN ADVISED OF THE POSSIBILITY OF SUCH DAMAGES. In any event, the total liability of the Rightsholder and CCC (including their respective employees and directors) shall not exceed the total amount actually paid by User for the relevant License. User assumes full liability for the actions and omissions of its principals, employees, agents, affiliates, successors, and assigns.

12) **Limited Warranties.** THE WORK(S) AND RIGHT(S) ARE PROVIDED "AS IS." CCC HAS THE RIGHT TO GRANT TO USER THE RIGHTS GRANTED IN THE ORDER CONFIRMATION

DOCUMENT. CCC AND THE RIGHTSHOLDER DISCLAIM ALL OTHER WARRANTIES RELATING TO THE WORK(S) AND RIGHT(S), EITHER EXPRESS OR IMPLIED, INCLUDING WITHOUT LIMITATION IMPLIED WARRANTIES OF MERCHANTABILITY OR FITNESS FOR A PARTICULAR PURPOSE. ADDITIONAL RIGHTS MAY BE REQUIRED TO USE ILLUSTRATIONS, GRAPH PHOTOGRAPHS, ABSTRACTS, INSERTS, OR OTHER PORTIONS OF THE WORK (AS OPPOSED TO THE ENTIRE WORK) IN A MANNER CONTEMPLATED BY USER; USER UNDERSTANDS AND AGREES THAT NEITHER CCC NOR THE RIGHTSHOLDER MAY HAVE SUCH ADDITIONAL RIGHTS TO GRANT.

13) Effect of Breach. Any failure by User to pay any amount when due, or any use by User of a Work beyond the scope of the License set forth in the Order Confirmation and/or the Terms, shall be a material breach of such License. Any breach not cured within 10 days of written notice thereof shall result in immediate termination of such License without further notice. Any unauthorized (but licensable) use of a Work that is terminated immediately upon notice thereof may be liquidated by payment of the Rightsholder's ordinary license price therefor; any unauthorized (and unlicensable) use that is not terminated immediately for any reason (including, for example, because materials containing the Work cannot reasonably be recalled) will be subject to all remedies available at law or in equity, but in no event to a payment of less than three times the Rightsholder's ordinary license price for the most closely analogous licensable use plus Rightsholder's and/or CCC's costs and expenses incurred in collecting such payment.

14) Additional Terms for Specific Products and Services. If a User is making one of the uses described in this Section 14, the additional terms and conditions apply:

a) *Print Uses of Academic Course Content and Materials (photocopies for academic coursepacks or classroom handouts).* For photocopies for academic coursepacks or classroom handouts the following additional terms apply:

i) The copies and anthologies created under this License may be made and assembled by faculty members individually or at their request by on-campus bookstores or copy centers, or by off-campus copy shops and other similar entities.

ii) No License granted shall in any way: (i) include any right by User to create a substantively non-identical copy of the Work or to edit or in any other way modify the Work (except by means of deleting material immediately preceding or following the entire portion of the Work copied) (ii) permit "publishing ventures" where any particular anthology would be systematically marketed at multiple institutions.

iii) Subject to any Publisher Terms (and notwithstanding any apparent contradiction in the Order Confirmation arising from data provided by User), any use authorized under the academic pay-per-use service is limited as follows:

A) any License granted shall apply to only one class (bearing a unique identifier as assigned by the institution, and thereby including all sections or other subparts of the class) at one institution;

B) use is limited to not more than 25% of the text of a book or of the items in a published collection of essays, poems or articles;

C) use is limited to no more than the greater of (a) 25% of the text of an issue of a journal or other periodical or (b) two articles from such an issue;

D) no User may sell or distribute any particular anthology, whether photocopied or electronic, at more than one institution of learning;

E) in the case of a photocopy permission, no materials may be entered into electronic memory by User except in order to produce an identical copy of a Work before or during the academic term (or analogous period) as to which any particular permission is granted. In the event that User shall choose to retain materials that are the subject of a photocopy permission in electronic memory for purposes of producing identical copies more than one day after such retention (but still within the scope of any permission granted), User must notify CCC of such fact in the applicable permission request and such retention shall constitute one copy actually sold for purposes of calculating permission fees due; and

F) any permission granted shall expire at the end of the class. No permission granted shall in any way include any right by User to create a substantively non-identical copy of the Work or to edit or in any other way modify the Work (except by means of deleting material immediately preceding or following the entire portion of the Work copied).

iv) Books and Records; Right to Audit. As to each permission granted under the academic pay-per-use Service, User shall maintain for at least four full calendar years books and records sufficient for CCC to determine the numbers of copies made by User under such permission. CCC and any representatives it may designate shall have the right to audit such books and records at any time during User's ordinary business hours, upon two days' prior notice. If any such audit shall determine that User shall have underpaid for, or underreported, any photocopies sold or by three percent (3%) or more, then User shall bear all the costs of any such audit; otherwise, CCC shall bear the costs of any such audit. Any amount determined by such audit to have been underpaid by User shall immediately be paid to CCC by User, together with interest thereon at the rate of 10% per annum from the date such amount was originally due. The provisions of this paragraph shall survive the termination of this License for any reason.

b) *Digital Pay-Per-Uses of Academic Course Content and Materials (e-coursepacks, electronic reserves, learning management systems, academic institution intranets).* For uses in e-coursepacks, posts in electronic reserves, posts in learning management systems, or posts on academic institution intranets, the following additional terms apply:

i) The pay-per-uses subject to this Section 14(b) include:

A) **Posting e-reserves, course management systems, e-coursepacks for text-based content**, which grants authorizations to import requested material in electronic format, and allows electronic access to this material to members of a designated college or university class, under the direction of an instructor designated by that college or university, accessible only under appropriate electronic controls (e.g., password);

B) **Posting e-reserves, course management systems, e-coursepacks for material consisting of photographs or other still images not embedded in text**, which grants not only the authorizations described in Section 14(b)(i)(A) above, but also the following authorization: to include the requested material in course materials for use consistent with Section 14(b)(i)(A) above, including any necessary resizing, reformatting or modification of the resolution of such requested material (provided that such modification does not alter the underlying editorial content or meaning of the requested material, and provided that the resulting modified content is used solely within the scope of, and in a manner consistent with, the particular authorization described in the Order Confirmation and the Terms), but not including any other form of manipulation, alteration or editing of the requested material;

C) **Posting e-reserves, course management systems, e-coursepacks or other academic distribution for audiovisual content**, which grants not only the authorization described in Section 14(b)(i)(A) above, but also the following authorizations: (i) to include the requested material in course materials for use consistent with Section 14(b)(i)(A) above; (ii) to display and perform the requested material to such members of such class in the physical classroom or remotely by means of streaming media or other video formats; and (iii) to "clip" or reformat the requested material for purposes of time or content management or ease of delivery, provided that such "clipping" or reformatting does not alter the underlying editorial content or meaning of the requested material and that the resulting material is used solely within the scope of, and in a manner consistent with, the particular authorization described in the Order Confirmation and the Terms. Unless expressly set forth in the relevant Order Confirmation, the License does not authorize any other form of manipulation, alteration or editing of the requested material.

ii) Unless expressly set forth in the relevant Order Confirmation, no License granted shall in any way: (i) include any right by User to create a substantively non-identical copy of the Work or to edit or in any other way modify the Work (except by means of deleting material immediately preceding or following the entire portion of the Work copied or, in the case of Works subject to Sections 14(b)(1)(B) or (C) above, as described in such Sections) (ii) permit "publishing ventures" where any particular course material would be systematically marketed at multiple institutions.

iii) Subject to any further limitations determined in the Rightsholder Terms (and notwithstanding any apparent contradiction in the Order Confirmation arising from data provided by User), any use authorized under the electronic course content pay-per-use service is limited as follows:

A) any License granted shall apply to only one class (bearing a unique identifier as assigned by the institution, and thereby including all sections or other subparts of the

class) at one institution;

B) use is limited to not more than 25% of the text of a book or of the items in a published collection of essays, poems or articles;

C) use is limited to not more than the greater of (a) 25% of the text of an issue of a journal or other periodical or (b) two articles from such an issue;

D) no User may sell or distribute any particular materials, whether photocopied or electronic, at more than one institution of learning;

E) electronic access to material which is the subject of an electronic-use permission must be limited by means of electronic password, student identification or other control permitting access solely to students and instructors in the class;

F) User must ensure (through use of an electronic cover page or other appropriate means) that any person, upon gaining electronic access to the material, which is the subject of a permission, shall see:

- a proper copyright notice, identifying the Rightsholder in whose name CCC has granted permission,
- a statement to the effect that such copy was made pursuant to permission,
- a statement identifying the class to which the material applies and notifying the reader that the material has been made available electronically solely for use in the class, and
- a statement to the effect that the material may not be further distributed to any person outside the class, whether by copying or by transmission and whether electronically or in paper form, and User must also ensure that such cover page or other means will print out in the event that the person accessing the material chooses to print out the material or any part thereof.

G) any permission granted shall expire at the end of the class and, absent some other form of authorization, User is thereupon required to delete the applicable material from any electronic storage or to block electronic access to the applicable material.

iv) Uses of separate portions of a Work, even if they are to be included in the same course material or the same university or college class, require separate permission under the electronic course content pay-per-use Service. Unless otherwise provided in the Order Confirmation, any grant of rights to User is limited to use completed no later than the end of the academic term (or analogous period) as to which any particular permission is granted.

v) Books and Records; Right to Audit. As to each permission granted under the electronic course content Service, User shall maintain for at least four full calendar years books and records sufficient for CCC to determine the numbers of copies made by User under such permission. CCC and any representatives it may designate shall have the right to audit such books and records at any time during User's ordinary business hours, upon two days' prior notice. If any such audit shall determine that User shall have underpaid for, or underreported, any electronic copies used by three percent (3%) or more, then User shall bear all the costs of any such audit; otherwise, CCC shall bear the costs of any such audit. Any amount determined by such audit to have been underpaid by User shall immediately be paid to CCC by User, together with interest thereon at the rate of 10% per annum from the date such amount was originally due. The provisions of this paragraph shall survive the termination of this license for any reason.

c) **Pay-Per-Use Permissions for Certain Reproductions (Academic photocopies for library reserves and interlibrary loan reporting) (Non-academic internal/external business uses and commercial document delivery).** The License expressly excludes the uses listed in Section (c)(i)-(v) below (which must be subject to separate license from the applicable Rightsholder) for: academic photocopies for library reserves and interlibrary loan reporting; and non-academic internal/external business uses and commercial document delivery.

i) electronic storage of any reproduction (whether in plain-text, PDF, or any other format) other than on a transitory basis;

ii) the input of Works or reproductions thereof into any computerized database;

iii) reproduction of an entire Work (cover-to-cover copying) except where the Work is a single article;

iv) reproduction for resale to anyone other than a specific customer of User;

v) republication in any different form. Please obtain authorizations for these uses through other CCC services or directly from the rightsholder.

Any license granted is further limited as set forth in any restrictions included in the Order Confirmation and/or in these Terms.

d) **Electronic Reproductions in Online Environments (Non-Academic-email, intranet, internet and extranet).** For "electronic reproductions", which generally includes e-mail use (including instant messaging or other electronic transmission to a defined group of recipients) or posting on an intranet, extranet or Intranet site (including any display or performance incidental thereto), the following additional terms apply:

i) Unless otherwise set forth in the Order Confirmation, the License is limited to use completed within 30 days for any use on the Internet, 60 days for any use on an intranet or extranet and one year for any other use, all as measured from the "republication date" as identified in the Order Confirmation, if any, and otherwise from the date of the Order Confirmation.

ii) User may not make or permit any alterations to the Work, unless expressly set forth in the Order Confirmation (after request by User and approval by Rightsholder provided, however, that a Work consisting of photographs or other still images not embedded in text may, if necessary, be resized, reformatted or have its resolution modified without additional express permission, and a Work consisting of audiovisual content may, if necessary, be "clipped" or reformatted for purposes of time or content management or ease of delivery (provided that any such resizing, reformatting, resolution modification or "clipping" does not alter the underlying editorial content or meaning of the Work used, and that the resulting material is used solely within the scope of, and in a manner consistent with, the particular License described in the Order Confirmation and the Terms.

15) Miscellaneous.

a) User acknowledges that CCC may, from time to time, make changes or additions to the Service or to the Terms, and that Rightsholder may make changes or additions to the Rightsholder Terms. Such updated Terms will replace the prior terms and conditions in the order workflow and shall be effective as to any subsequent Licenses but shall not apply to Licenses already granted and paid for under a prior set of terms.

b) Use of User-related information collected through the Service is governed by CCC's privacy policy, available online at www.copyright.com/about/privacy-policy/.

c) The License is personal to User. Therefore, User may not assign or transfer to any other person (whether a natural person or an organization of any kind) the License or the rights granted thereunder; provided, however, that, where applicable, User may assign such License in its entirety on written notice to CCC in the event of a transfer of all or substantially all of User's rights in any new material which includes the Work(s) licensed under this Service.

d) No amendment or waiver of any Terms is binding unless set forth in writing and signed by the appropriate parties, including, where applicable, the Rightsholder. The Rightsholder and CCC hereby object to any terms contained in any writing prepared by or on behalf of the User or its principals, employees, agents or affiliates and purporting

to govern or otherwise relate to the License described in the Order Confirmation, which terms are in any way inconsistent with any Terms set forth in the Order Confirmation and/or in CCC's standard operating procedures, whether such writing is prepared prior to, simultaneously with or subsequent to the Order Confirmation, and whether such writing appears on a copy of the Order Confirmation or in a separate instrument.

e) The License described in the Order Confirmation shall be governed by and construed under the law of the State of New York, USA, without regard to the principles thereof conflicts of law. Any case, controversy, suit, action, or proceeding arising out of, in connection with, or related to such License shall be brought, at CCC's sole discretion, in a federal or state court located in the County of New York, State of New York, USA, or in any federal or state court whose geographical jurisdiction covers the location of the Rightsholder set forth in the Order Confirmation. The parties expressly submit to the personal jurisdiction and venue of each such federal or state court.

Last updated October 2022





Order Number: 1388681

Order Date: 22 Aug 2023

Payment Information

Merve Kiniklioğlu
mervekiniklioglu@gmail.com
Payment method: Invoice

Billing Address:
Merve Kiniklioğlu
Bilkent University Aysel Sabuncu Brain Research
Center
Ankara, 06800
Turkey

+90 (506)6389525
mervekiniklioglu@gmail.com

Customer Location:
Merve Kiniklioğlu
Bilkent University Aysel Sabuncu Brain Research
Center
Ankara, 06800
Turkey

Order Details

1. Principles of neural science

Billing Status:
Open

Order License ID	1388681-1	Type of Use	Republish in a thesis/dissertation
Order detail status	Completed	Publisher	MCGRAW-HILL
ISBN-13	9780071390118	Portion	Chart/graph/table/figure
			0.00 US
			Republication Permission

LICENSED CONTENT

Publication Title	Principles of neural science	Language	English
Author/Editor	KANDEL, ERIC R.	Rightsholder	McGraw Hill LLC
Date	01/01/2013	Publication Type	Book

REQUEST DETAILS

Portion Type	Chart/graph/table/figure	Distribution	Worldwide
Number of Charts / Graphs / Tables / Figures Requested	1	Translation	Original language of publication
Format (select all that apply)	Print, Electronic	Copies for the Disabled?	No
Who Will Republish the Content?	Academic institution	Minor Editing Privileges?	No
Duration of Use	Life of current and all future editions	Incidental Promotional Use?	No
Lifetime Unit Quantity	Up to 2,000,000	Currency	USD
Rights Requested	Main product		

NEW WORK DETAILS

Title	BEHAVIORAL AND NEURAL INVESTIGATION ON THE EFFECT OF SPATIAL ATTENTION ON SURROUND SUPPRESSION	Institution Name	Bilkent University
		Expected Presentation Date	2023-09-22
Instructor Name	Merve Kiniklioğlu		

ADDITIONAL DETAILS

The Requesting Person/Organization to Appear on the License	Merve Kiniklioğlu
---	-------------------

REQUESTED CONTENT DETAILS

Title, Description or Numeric Reference of the Portion(s)	Figure 25-14 Parallel processing in visual pathways.	Title of the Article/Chapter the Portion Is From	The Constructive Nature of Visual Processing
Editor of Portion(s)	Charles D. Gilbert	Author of Portion(s)	KANDEL, ERIC R.
Volume / Edition	5th	Publication Date of Portion	2013-01-01
Page or Page Range of Portion	571		

McGraw Hill LLC Terms and Conditions

It is the responsibility of the user to verify that the text, figures, images and other material that they wish to use are owned by McGraw Hill LLC. McGraw Hill LLC can only grant permission for the material that they own. Please check the caption of any figures, images, charts, etc., as well as any credits pages at the front or back of the book. McGraw Hill LLC may restrict the portion of the title that may be used.

Total Items: 1

Subtotal: 0.00 US
Order Total: 0.00 US

Marketplace Permissions General Terms and Conditions

The following terms and conditions ("General Terms"), together with any applicable Publisher Terms and Conditions, govern User's use of Works pursuant to the Licenses granted by Copyright Clearance Center, Inc. ("CCC") on behalf of the applicable Rightsholders of such Works through CCC's applicable Marketplace transactional licensing services (each, "Service").

1) **Definitions.** For purposes of these General Terms, the following definitions apply:

"License" is the licensed use the User obtains via the Marketplace platform in a particular licensing transaction, as set forth in the Order Confirmation.

"Order Confirmation" is the confirmation CCC provides to the User at the conclusion of each Marketplace transaction. "Order Confirmation Terms" are additional terms set forth in specific Order Confirmations not set forth in the General Terms that can include terms applicable to a particular CCC transactional licensing service and/or any Rightsholder-specific terms.

"Rightsholder(s)" are the holders of copyright rights in the Works for which a User obtains licenses via the Marketplace platform, which are displayed on specific Order Confirmations.

"Terms" means the terms and conditions set forth in these General Terms and any additional Order Confirmation Terms collectively.

"User" or "you" is the person or entity making the use granted under the relevant License. Where the person accepting the Terms on behalf of a User is a freelancer or other third party who the User authorized to accept the General Terms on the User's behalf, such person shall be deemed jointly a User for purposes of such Terms.

"Work(s)" are the copyright protected works described in relevant Order Confirmations.

2) **Description of Service.** CCC's Marketplace enables Users to obtain Licenses to use one or more Works in accordance with all relevant Terms. CCC grants Licenses as an agent on behalf of the copyright rightsholder identified in the relevant Order Confirmation.

3) **Applicability of Terms.** The Terms govern User's use of Works in connection with the relevant License. In the event of any conflict between General Terms and Order Confirmation Terms, the latter shall govern. User acknowledges that Rightsholders have complete discretion whether to grant any permission, and whether to place any limitation on any grant, and that CCC has no right to supersede or to modify any such discretionary act by a Rightsholder.

4) **Representations; Acceptance.** By using the Service, User represents and warrants that User has been duly authorized by the User to accept, and hereby does accept, all Terms

5) **Scope of License; Limitations and Obligations.** All Works and all rights therein, including copyright rights, remain the sole and exclusive property of the Rightsholder. The License provides only those rights expressly set forth in the terms and conveys no other rights in any Works

6) **General Payment Terms.** User may pay at time of checkout by credit card or choose to be invoiced. If the User chooses to be invoiced, the User shall: (i) remit payments in the manner identified on specific invoices, (ii) unless otherwise specifically stated in an Order Confirmation or separate written agreement, Users shall remit payments upon receipt of the relevant invoice from CCC, either by delivery or notification of availability of the invoice via the Marketplace platform, and (iii) if the User does not pay the invoice within 30 days of receipt, the User may incur a service charge of 1.5% per month or the maximum rate allowed by applicable law, whichever is less. While User may exercise the rights in the License immediately upon receiving the Order Confirmation, the License is automatically revoked and is null and void, as if it had never been issued, if CCC does not receive complete payment on a timely basis.

7) **General Limits on Use.** Unless otherwise provided in the Order Confirmation, any grant of rights to User (i) involves only the rights set forth in the Terms and does not include subsequent or additional uses, (ii) is non-exclusive and non-transferable, and (iii) is subject to any and all limitations and restrictions (such as, but not limited to, limitations on duration of use or circulation) included in the Terms. Upon completion of the licensed use as set forth in the Order Confirmation, User shall either secure a new permission for further use of the Work(s) or immediately cease any new use of the Work(s) and shall render inaccessible (such as by deleting or by removing or severing links or other locators) all further copies of the Work. User may only make alterations to the Work if and as expressly set forth in the Order Confirmation. No Work may be used in any way that is unlawful including without limitation if such use would violate applicable sanctions laws or regulations, would be defamatory, violate the rights of third parties (including such third parties' rights of copyright, privacy, publicity, or other tangible or intangible property), or is otherwise illegal, sexually explicit, or obscene. In addition, User may not conjoin a Work with any other material that may result in damage to the reputation of the Rightsholder. Any unlawful use will render any licenses hereunder null and void. User agrees to inform CCC if becomes aware of any infringement of any rights in a Work and to cooperate with any reasonable request of CCC or the Rightsholder in connection therewith.

8) **Third Party Materials.** In the event that the material for which a License is sought includes third party materials (such as photographs, illustrations, graphs, inserts and similar materials) that are identified in such material as having been used by permission (or a similar indicator), User is responsible for identifying, and seeking separate licenses (under this Service, if available, or otherwise) for any of such third party materials; without a separate license, User may not use such third party materials via the License.

9) **Copyright Notice.** Use of proper copyright notice for a Work is required as a condition of any License granted under the Service. Unless otherwise provided in the Order Confirmation, a proper copyright notice will read substantially as follows: "Used with permission of [Rightsholder's name], from [Work's title, author, volume, edition number and year of copyright]; permission conveyed through Copyright Clearance Center, Inc." Such notice must be provided in a reasonably legible font size and must be placed either on cover page or in another location that any person, upon gaining access to the material which is the subject of a permission, shall see, or in the case of republication License immediately adjacent to the Work as used (for example, as part of a by-line or footnote) or in the place where substantially all other credits or notices for the new work containing the republished Work are located. Failure to include the required notice results in loss to the Rightsholder and CCC, and the User shall be liable to pay liquidated damages for each such failure equal to twice the use fee specified in the Order Confirmation, in addition to the use fee itself and any other fees and charges specified.

10) **Indemnity.** User hereby indemnifies and agrees to defend the Rightsholder and CCC, and their respective employees and directors, against all claims, liability, damages, costs and expenses, including legal fees and expenses, arising out of any use of a Work beyond the scope of the rights granted herein and in the Order Confirmation, or any use of Work which has been altered in any unauthorized way by User, including claims of defamation or infringement of rights of copyright, publicity, privacy, or other tangible or intangible property.

11) **Limitation of Liability.** UNDER NO CIRCUMSTANCES WILL CCC OR THE RIGHTSHOLDER BE LIABLE FOR ANY DIRECT, INDIRECT, CONSEQUENTIAL, OR INCIDENTAL DAMAGES (INCLUDING WITHOUT LIMITATION DAMAGES FOR LOSS OF BUSINESS PROFITS OR INFORMATION, OR FOR BUSINESS INTERRUPTION) ARISING OUT OF THE USE OR INABILITY TO USE A WORK, EVEN IF ONE OR BOTH OF THEM HAS BEEN ADVISED OF THE POSSIBILITY OF SUCH DAMAGES. In any event, the total liability of the Rightsholder and CCC (including their respective employees and directors) shall not exceed the total amount actually paid by User for the relevant License. User assumes full liability for the actions and omissions of its principals, employees, agents, affiliates, successors, and assigns.

12) **Limited Warranties.** THE WORK(S) AND RIGHT(S) ARE PROVIDED "AS IS." CCC HAS THE RIGHT TO GRANT TO USER THE RIGHTS GRANTED IN THE ORDER CONFIRMATION DOCUMENT. CCC AND THE RIGHTSHOLDER DISCLAIM ALL OTHER WARRANTIES RELATING TO THE WORK(S) AND RIGHT(S), EITHER EXPRESS OR IMPLIED, INCLUDING WITHOUT LIMITATION IMPLIED WARRANTIES OF MERCHANTABILITY OR FITNESS FOR A PARTICULAR PURPOSE. ADDITIONAL RIGHTS MAY BE REQUIRED TO USE ILLUSTRATIONS, GRAPH PHOTOGRAPHS, ABSTRACTS, INSERTS, OR OTHER PORTIONS OF THE WORK (AS OPPOSED TO THE ENTIRE WORK) IN A MANNER CONTEMPLATED BY USER; USER UNDERSTANDS AND AGREES THAT NEITHER CCC NOR THE RIGHTSHOLDER MAY HAVE SUCH ADDITIONAL RIGHTS TO GRANT.

13) **Effect of Breach.** Any failure by User to pay any amount when due, or any use by User of a Work beyond the scope of the License set forth in the Order Confirmation and/or the Terms, shall be a material breach of such License. Any breach not cured within 10 days of written notice thereof shall result in immediate termination of such License without further notice. Any unauthorized (but licensable) use of a Work that is terminated immediately upon notice thereof may be liquidated by payment of the Rightsholder's ordinary license price therefor; any unauthorized (and unlicensable) use that is not terminated immediately for any reason (including, for example, because materials containing the Work cannot reasonably be recalled) will be subject to all remedies available at law or in equity, but in no event to a payment of less than three times the Rightsholder's ordinary license price for the most closely analogous licensable use plus Rightsholder's and/or CCC's costs and expenses incurred in collecting such payment.

14) **Additional Terms for Specific Products and Services.** If a User is making one of the uses described in this Section 14, the additional terms and conditions apply:

a) **Print Uses of Academic Course Content and Materials (photocopies for academic coursepacks or classroom handouts).** For photocopies for academic coursepacks or classroom handouts the following additional terms apply:

i) The copies and anthologies created under this License may be made and assembled by faculty members individually or at their request by on-campus bookstores or copy centers, or by off-campus copy shops and other similar entities.

ii) No License granted shall in any way: (i) include any right by User to create a substantively non-identical copy of the Work or to edit or in any other way modify the Work (except by means of deleting material immediately preceding or following the entire portion of the Work copied) (ii) permit "publishing ventures" where any particular anthology would be systematically marketed at multiple institutions.

iii) Subject to any Publisher Terms (and notwithstanding any apparent contradiction in the Order Confirmation arising from data provided by User), any use authorized under the academic pay-per-use service is limited as follows:

A) any License granted shall apply to only one class (bearing a unique identifier as assigned by the institution, and thereby including all sections or other subparts of the class) at one institution;

B) use is limited to not more than 25% of the text of a book or of the items in a published collection of essays, poems or articles;

C) use is limited to no more than the greater of (a) 25% of the text of an issue of a journal or other periodical or (b) two articles from such an issue;

D) no User may sell or distribute any particular anthology, whether photocopied or electronic, at more than one institution of learning;

E) in the case of a photocopy permission, no materials may be entered into electronic memory by User except in order to produce an identical copy of a Work before or during the academic term (or analogous period) as to which any particular permission is granted. In the event that User shall choose to retain materials that are the subject of a photocopy permission in electronic memory for purposes of producing identical copies more than one day after such retention (but still within the scope of any permission granted), User must notify CCC of such fact in the applicable permission request and such retention shall constitute one copy actually sold for purposes of calculating permission fees due; and

F) any permission granted shall expire at the end of the class. No permission granted shall in any way include any right by User to create a substantively non-identical copy of the Work or to edit or in any other way modify the Work (except by means of deleting material immediately preceding or following the entire portion of the Work copied).

iv) **Books and Records; Right to Audit.** As to each permission granted under the academic pay-per-use Service, User shall maintain for at least four full calendar years books and records sufficient for CCC to determine the numbers of copies made by User under such permission. CCC and any representatives it may designate shall have the right to audit such books and records at any time during User's ordinary business hours, upon two days' prior notice. If any such audit shall determine that User shall have underpaid for, or underreported, any photocopies sold or by three percent (3%) or more, then User shall bear all the costs of any such audit; otherwise, CCC shall bear the costs of any such audit. Any amount determined by such audit to have been underpaid by User shall immediately be paid to CCC by User, together with interest thereon at the rate of 10% per annum from the date such amount was originally due. The provisions of this paragraph shall survive the termination of this License for any reason.

b) **Digital Pay-Per-Uses of Academic Course Content and Materials (e-coursepacks, electronic reserves, learning management systems, academic institution intranets).** For uses in e-coursepacks, posts in electronic reserves, posts in learning management systems, or posts on academic institution intranets, the following additional terms apply:

i) The pay-per-uses subject to this Section 14(b) include:

A) **Posting e-reserves, course management systems, e-coursepacks for text-based content**, which grants authorizations to import requested material in electronic format, and allows electronic access to this material to members of a designated college or university class, under the direction of an instructor designated by the college or university, accessible only under appropriate electronic controls (e.g., password);

B) **Posting e-reserves, course management systems, e-coursepacks for material consisting of photographs or other still images not embedded in text**, which grants not only the authorizations described in Section 14(b)(i)(A) above, but also the following authorization: to include the requested material in course materials for use consistent with Section 14(b)(i)(A) above, including any necessary resizing, reformatting or modification of the resolution of such requested material (provided that such modification does not alter the underlying editorial content or meaning of the requested material, and provided that the resulting modified content is used solely within the scope of, and in a manner consistent with, the particular authorization described in the Order Confirmation and the Terms), but not including any other form of manipulation, alteration or editing of the requested material;

C) **Posting e-reserves, course management systems, e-coursepacks or other academic distribution for audiovisual content**, which grants not only the authorization described in Section 14(b)(i)(A) above, but also the following authorizations: (i) to include the requested material in course materials for use consistent with Section 14(b)(i)(A) above; (ii) to display and perform the requested material to such members of such class in the physical classroom or remotely by means of streaming media or other video formats; and (iii) to "clip" or reformat the requested material for purposes of time or content management or ease of delivery, provided that such "clipping" or reformatting does not alter the underlying editorial content or meaning of the requested material and that the resulting material is used solely within the scope of, and in a manner consistent with, the particular authorization described in the Order Confirmation and the Terms. Unless expressly set forth in the relevant Order Confirmation, the License does not authorize any other form of manipulation, alteration or editing of the requested material.

ii) Unless expressly set forth in the relevant Order Confirmation, no License granted shall in any way: (i) include any right by User to create a substantively non-identical copy of the Work or to edit or in any other way modify the Work (except by means of deleting material immediately preceding or following the entire portion of the Work copied) or, in the case of Works subject to Sections 14(b)(1)(B) or (C) above, as described in such Sections) (ii) permit "publishing ventures" where any particular course material would be systematically marketed at multiple institutions.

iii) Subject to any further limitations determined in the Rightsholder Terms (and notwithstanding any apparent contradiction in the Order Confirmation arising from data provided by User), any use authorized under the electronic course content pay-per-use service is limited as follows:

A) any License granted shall apply to only one class (bearing a unique identifier as assigned by the institution, and thereby including all sections or other subparts of the class) at one institution;

B) use is limited to not more than 25% of the text of a book or of the items in a published collection of essays, poems or articles;

C) use is limited to not more than the greater of (a) 25% of the text of an issue of a journal or other periodical or (b) two articles from such an issue;

D) no User may sell or distribute any particular materials, whether photocopied or electronic, at more than one institution of learning;

E) electronic access to material which is the subject of an electronic-use permission must be limited by means of electronic password, student identification or other control permitting access solely to students and instructors in the class;

F) User must ensure (through use of an electronic cover page or other appropriate means) that any person, upon gaining electronic access to the material, which is the subject of a permission, shall see:

- o a proper copyright notice, identifying the Rightsholder in whose name CCC has granted permission,
- o a statement to the effect that such copy was made pursuant to permission,
- o a statement identifying the class to which the material applies and notifying the reader that the material has been made available electronically solely for use in the class, and
- o a statement to the effect that the material may not be further distributed to any person outside the class, whether by copying or by transmission and whether electronically or in paper form, and User must also ensure that such cover page or other means will print out in the event that the person accessing the material chooses to print out the material or any part thereof.

G) any permission granted shall expire at the end of the class and, absent some other form of authorization, User is thereupon required to delete the applicable material from any electronic storage or to block electronic access to the applicable material.

iv) Uses of separate portions of a Work, even if they are to be included in the same course material or the same university or college class, require separate permission under the electronic course content pay-per-use Service. Unless otherwise provided in the Order Confirmation, any grant of rights to User is limited to use completed no later than the end of the academic term (or analogous period) as to which any particular permission is granted.

v) Books and Records; Right to Audit. As to each permission granted under the electronic course content Service, User shall maintain for at least four full calendar years books and records sufficient for CCC to determine the numbers of copies made by User under such permission. CCC and any representatives it may designate shall have the right to audit such books and records at any time during User's ordinary business hours, upon two days' prior notice. If any such audit shall determine that User shall have underpaid for, or underreported, any electronic copies used by three percent (3%) or more, then User shall bear all the costs of any such audit; otherwise, CCC shall bear the costs of any such audit. Any amount determined by such audit to have been underpaid by User shall immediately be paid to CCC by User, together with interest thereon at the rate of 10% per annum from the date such amount was originally due. The provisions of this paragraph shall survive the termination of this license for any reason.

c) **Pay-Per-Use Permissions for Certain Reproductions (Academic photocopies for library reserves and interlibrary loan reporting) (Non-academic internal/external business uses and commercial document delivery).** The License expressly excludes the uses listed in Section (c)(i)-(v) below (which must be subject to separate license from the applicable Rightsholder) for: academic photocopies for library reserves and interlibrary loan reporting; and non-academic internal/external business uses and commercial document delivery.

i) electronic storage of any reproduction (whether in plain-text, PDF, or any other format) other than on a transitory basis;

ii) the input of Works or reproductions thereof into any computerized database;

iii) reproduction of an entire Work (cover-to-cover copying) except where the Work is a single article;

iv) reproduction for resale to anyone other than a specific customer of User;

v) republication in any different form. Please obtain authorizations for these uses through other CCC services or directly from the rightsholder.

Any license granted is further limited as set forth in any restrictions included in the Order Confirmation and/or in these Terms.

d) **Electronic Reproductions in Online Environments (Non-Academic-email, intranet, internet and extranet).** For "electronic reproductions", which generally includes e-mail use (including instant messaging or other electronic transmission to a defined group of recipients) or posting on an intranet, extranet or Intranet site (including any display or performance incidental thereto), the following additional terms apply:

i) Unless otherwise set forth in the Order Confirmation, the License is limited to use completed within 30 days for any use on the Internet, 60 days for any use on an intranet or extranet and one year for any other use, all as measured from the "republication date" as identified in the Order Confirmation, if any, and otherwise from the date of the Order Confirmation.

ii) User may not make or permit any alterations to the Work, unless expressly set forth in the Order Confirmation (after request by User and approval by Rightsholder provided, however, that a Work consisting of photographs or other still images not embedded in text may, if necessary, be resized, reformatted or have its resolution modified without additional express permission, and a Work consisting of audiovisual content may, if necessary, be "clipped" or reformatted for purposes of time or content management or ease of delivery (provided that any such resizing, reformatting, resolution modification or "clipping" does not alter the underlying editorial content or meaning of the Work used, and that the resulting material is used solely within the scope of, and in a manner consistent with, the particular License described in the Order Confirmation and the Terms.

15) Miscellaneous.

a) User acknowledges that CCC may, from time to time, make changes or additions to the Service or to the Terms, and that Rightsholder may make changes or additions to the Rightsholder Terms. Such updated Terms will replace the prior terms and conditions in the order workflow and shall be effective as to any subsequent Licenses but shall not apply to Licenses already granted and paid for under a prior set of terms.

b) Use of User-related information collected through the Service is governed by CCC's privacy policy, available online at www.copyright.com/about/privacy-policy/.

c) The License is personal to User. Therefore, User may not assign or transfer to any other person (whether a natural person or an organization of any kind) the License or any rights granted thereunder; provided, however, that, where applicable, User may assign such License in its entirety on written notice to CCC in the event of a transfer of all or substantially all of User's rights in any new material which includes the Work(s) licensed under this Service.

d) No amendment or waiver of any Terms is binding unless set forth in writing and signed by the appropriate parties, including, where applicable, the Rightsholder. If Rightsholder and CCC hereby object to any terms contained in any writing prepared by or on behalf of the User or its principals, employees, agents or affiliates and purporting to govern or otherwise relate to the License described in the Order Confirmation, which terms are in any way inconsistent with any Terms set forth in the Order Confirmation and/or in CCC's standard operating procedures, whether such writing is prepared prior to, simultaneously with or subsequent to the Order Confirmation, and whether such writing appears on a copy of the Order Confirmation or in a separate instrument.

e) The License described in the Order Confirmation shall be governed by and construed under the law of the State of New York, USA, without regard to the principles thereof conflicts of law. Any case, controversy, suit, action, or proceeding arising out of, in connection with, or related to such License shall be brought, at CCC's sole discretion, in any

federal or state court located in the County of New York, State of New York, USA, or in any federal or state court whose geographical jurisdiction covers the location of the Rightsholder set forth in the Order Confirmation. The parties expressly submit to the personal jurisdiction and venue of each such federal or state court.

Last updated October 2022



Bibliography

- [1] O. S. Dhande, B. K. Stafford, J. A. Lim, and A. D. Huberman, “Contributions of retinal ganglion cells to subcortical visual processing and behaviors,” *Annual review of vision science*, vol. 1, pp. 291–328, 2015.
- [2] E. R. Kandel, J. H. Schwartz, T. M. Jessell, D. of Biochemistry, M. B. T. Jessell, S. Siegelbaum, and A. Hudspeth, *Principles of neural science*, vol. 4. McGraw-hill New York, 2000.
- [3] K. Herrmann, L. Montaser-Kouhsari, M. Carrasco, and D. J. Heeger, “When size matters: attention affects performance by contrast or response gain,” *Nature Neuroscience*, vol. 13, no. 12, pp. 1554–1559, 2010.
- [4] J. H. Reynolds and D. J. Heeger, “The normalization model of attention,” *Neuron*, vol. 61, no. 2, pp. 168–185, 2009.
- [5] F. Hutmacher, “Why is there so much more research on vision than on any other sensory modality?,” *Frontiers in Psychology*, vol. 10, pp. 1–47, 2019.
- [6] G. Pike, G. Edgar, and H. Edgar, *Perception*, pp. 65–69. Oxford: Oxford University Press, 2012.
- [7] K. J. H., “The evolution of the complex sensory and motor systems of the human brain,” *Brain research bulletin*, vol. 75, no. 2-4, pp. 384–390, 2008.
- [8] D. C. Van Essen, D. J. Felleman, E. A. DeYoe, J. Olavarria, and J. Knierim, “Modular and hierarchical organization of extrastriate visual cortex in the macaque monkey,” *Cold Spring Harb. Symp. Quant. Biol.*, vol. 55, pp. 679–696, 1990.

- [9] F. D. J. and V. E. D.C., “Distributed hierarchical processing in the primate cerebral cortex,” *Cerebral Cortex*, vol. 1, pp. 1–47, 1991.
- [10] J. E. Dowling and B. B. Boycott, “Organization of the primate retina: electron microscopy,” *Proceedings of the Royal Society of London. Series B. Biological sciences*, vol. 166, no. 11, pp. 80–111, 1966.
- [11] D. A. Baylor, “Photoreceptor signals and vision. proctor lecture,” *Investigative ophthalmology & visual science*, vol. 28, pp. 34–39, 1987.
- [12] K. W. Yau, “Phototransduction mechanism in retinal rods and cones.the friedenwald lecture,” *Investigative ophthalmology & visual science*, vol. 35, no. 1, pp. 9–32, 1994.
- [13] D. Purves, G. J. Augustine, D. Fitzpatrick, W. C. Hall, A.-S. LaMantia, J. O. McNamara, and S. M. Williams, eds., *Neuroscience*, 3rd ed. Sinauer Associates, 2004.
- [14] D. H. Hubel and T. N. Wiesel, “Receptive fields of single neurones in the cat’s striate cortex,” *Journal of physiology*, vol. 148, no. 3, pp. 574–591, 1959.
- [15] P. H. Schiller, J. H. Sandell, and J. H. Maunsell, “Functions of the on and off channels of the visual system,” *Nature* 1986 322:6082, vol. 322, pp. 824–825, 1986.
- [16] S. W. Kuffler, “Discharge patterns and functional organization of mammalian retina,” *Journal of neurophysiology*, vol. 16, no. 1, pp. 37–68, 1953.
- [17] G. von Békésy, “Mach band type lateral inhibition in different sense organs,” *The Journal of general physiology*, vol. 50, no. 3, pp. 519–532, 1967.
- [18] L. Squire, D. Berg, F. E. Bloom, S. Du Lac, A. Ghosh, and N. C. Spitzer, *Fundamental neuroscience*. Academic press, 2012.
- [19] B. F., “Role of feedback connections in central visual processing,” *Annual review of vision science*, vol. 6, pp. 313–334, 2020.

- [20] P. H. Schiller and E. J. Tehovnik, “The Lateral Geniculate Nucleus,” in *Vision and the Visual System*, Oxford University Press, 08 2015.
- [21] D. C. Van Essen, C. H. Anderson, and D. J. Felleman, “Information processing in the primate visual system: an integrated systems perspective,” *Science*, vol. 255, no. 5043, pp. 419–423, 1992.
- [22] D. H. Hubel and T. N. Wiesel, “Receptive fields, binocular interaction and functional architecture in the cat’s visual cortex,” *The Journal of physiology*, vol. 160, no. 1, p. 106, 1962.
- [23] D. H. Hubel and T. N. Wiesel, “Receptive fields and functional architecture of monkey striate cortex,” *J. Physiol*, vol. 195, pp. 215–243, 1968.
- [24] D. H. Hubel and T. N. Wiesel, “Early exploration of the visual cortex,” *Neuron*, vol. 20, pp. 401–412, 1998.
- [25] H. B. Barlow, C. Blakemore, and J. D. Pettigrew, “The neural mechanism of binocular depth discrimination,” *The Journal of Physiology*, vol. 193, p. 327, 11 1967.
- [26] B. G. Cumming, “An unexpected specialization for horizontal disparity in primate primary visual cortex,” *Nature*, vol. 418, pp. 633–636, 8 2002.
- [27] D. H. Hubel, T. N. Wiesel, and M. P. Stryker, “Anatomical demonstration of orientation columns in macaque monkey,” *Journal of Comparative Neurology*, vol. 177, no. 3, pp. 361–379, 1978.
- [28] J. C. Horton and D. H. Hubel, “Regular patchy distribution of cytochrome oxidase staining in primary visual cortex of macaque monkey,” *Nature*, vol. 292, no. 5825, pp. 762–764, 1981.
- [29] M. Mishkin and L. G. Ungerleider, “Contribution of striate inputs to the visuospatial functions of parieto-preoccipital cortex in monkeys,” *Behavioural Brain Research*, vol. 6, pp. 57–77, 9 1982.
- [30] M. A. Goodale and G. K. Humphrey, “The objects of action and perception,” *Cognition*, vol. 67, pp. 181–207, 7 1998.

- [31] W. T. Newsome and E. B. Pare, "A selective impairment of motion perception following lesions of the middle temporal visual area (mt)," *Journal of Neuroscience*, vol. 8, no. 6, pp. 2201–2211, 1988.
- [32] C. D. Salzman, C. M. Murasugi, K. H. Britten, and W. T. Newsome, "Microstimulation in visual area mt: effects on direction discrimination performance," *Journal of Neuroscience*, vol. 12, no. 6, pp. 2331–2355, 1992.
- [33] D. J. McKeefry, M. P. Burton, C. Vakrou, B. T. Barrett, and A. B. Morland, "Induced deficits in speed perception by transcranial magnetic stimulation of human cortical areas v5/mt+ and v3a," *Journal of Neuroscience*, vol. 28, no. 27, pp. 6848–6857, 2008.
- [34] S. M. Zeki, "Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey," *The Journal of Physiology*, vol. 236, pp. 549–573, 2 1974.
- [35] T. D. Albright, "Direction and orientation selectivity of neurons in visual area mt of the macaque," *Journal of neurophysiology*, vol. 52, no. 6, pp. 1106–1130, 1984.
- [36] S. E. Petersen, J. F. Baker, and J. M. Allman, "Dimensional selectivity of neurons in the dorsolateral visual area of the owl monkey," *Brain Research*, vol. 197, pp. 507–511, 1980.
- [37] J. H. Maunsell and D. C. Van Essen, "Functional properties of neurons in middle temporal visual area of the macaque monkey. i. selectivity for stimulus direction, speed, and orientation," *Journal of neurophysiology*, vol. 49, no. 5, pp. 1127–1147, 1983.
- [38] D. Malonek, R. B. H. Tootell, and A. Grinvald, "Optical imaging reveals the functional architecture of neurons processing shape and motion in owl monkey area mt," *Proceedings: Biological Sciences*, vol. 258, no. 1352, pp. 109–119, 1994.
- [39] J. Allman, F. Miezin, and E. McGuinness, "Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (mt)," *Perception*, vol. 14, pp. 105–126, 1985.

- [40] S. Raiguel, M. Van Hulle, D.-K. Xiao, V. Marcar, and G. A. Orban, “Shape and spatial distribution of receptive fields and antagonistic motion surrounds in the middle temporal area (v5) of the macaque,” *European journal of neuroscience*, vol. 7, no. 10, pp. 2064–2082, 1995.
- [41] J. F. Baker, S. E. Petersen, W. T. Newsome, and J. M. Allman, “Visual response properties of neurons in four extrastriate visual areas of the owl monkey (*aotus trivirgatus*): a quantitative comparison of medial, dorsomedial, dorsolateral, and middle temporal areas,” *Journal of Neurophysiology*, vol. 45, no. 3, pp. 397–416, 1981.
- [42] T. D. Albright, “Form-cue invariant motion processing in primate visual cortex,” *Science (New York, N.Y.)*, vol. 255, pp. 1141–1143, 1992.
- [43] M. B. Wall, A. Lingnau, H. Ashida, and A. T. Smith, “elective visual responses to expansion and rotation in the human mt complex revealed by functional magnetic resonance imaging adaptation,” *The European journal of neuroscience*, vol. 27, no. 10, pp. 2747–2757, 2008.
- [44] C. J. Duffy and R. H. Wurtz, “Response of monkey mst neurons to optic flow stimuli with shifted centers of motion,” *Journal of Neuroscience*, vol. 15, no. 7, pp. 5192–5208, 1995.
- [45] A. Smith, M. Wall, A. Williams, and K. D. Singh, “Sensitivity to optic flow in human cortical areas mt and mst,” *European Journal of Neuroscience*, vol. 23, no. 2, pp. 561–569, 2006.
- [46] Y. Gu, G. C. DeAngelis, and D. E. Angelaki, “A functional link between area mstd and heading perception based on vestibular signals,” *Nature neuroscience*, vol. 10, no. 8, pp. 1038–1047, 2007.
- [47] T. D. Albright and R. Desimone, “Local precision of visuotopic organization in the middle temporal area (mt) of the macaque,” *Experimental brain research*, vol. 65, no. 3, pp. 582–592, 1987.
- [48] S. L. Strong, E. H. Silson, A. D. Gouws, A. B. Morland, and D. J. McKeefry, “A direct demonstration of functional differences between subdivisions of human v5/mt,” *Cerebral cortex*, vol. 27, no. 1, pp. 1–10, 2017.

- [49] V. A. Lamme, H. Super, and H. Spekreijse, “Feedforward, horizontal, and feedback processing in the visual cortex,” *Current opinion in neurobiology*, vol. 8, no. 4, pp. 529–535, 1998.
- [50] A. Angelucci and P. C. Bressloff, “The contribution of feedforward, lateral and feedback connections to the classical receptive field center and extra-classical receptive field surround of primate v1 neurons,” *Progress in Brain Research*, vol. 154, pp. 93–120, 2006.
- [51] J. Bullier, J. M. Hupé, A. C. James, and P. Girard, “The role of feedback connections in shaping the responses of visual cortical neurons,” *Progress in brain research*, vol. 134, pp. 193–204, 2001.
- [52] V. A. Lamme, H. Supèr, R. Landman, P. R. Roelfsema, and H. Spekreijse, “The role of primary visual cortex (v1) in visual awareness,” *Vision Research*, vol. 40, pp. 1507–1521, 2001.
- [53] E. A. Buffalo, P. Fries, R. Landman, H. Liang, and R. Desimone, “A backward progression of attentional effects in the ventral stream,” *PNAS*, vol. 107, pp. 361–365, 2010.
- [54] G. G. Gregoriou, S. J. Gotts, H. Zhou, and R. Desimone, “High-frequency, long-range coupling between prefrontal and visual cortex during attention,” *Science*, vol. 324, pp. 1207–1210, 2009.
- [55] B. Noudoost, M. H. Chang, N. A. Steinmetz, and T. Moore, “Top-down control of visual attention,” *Curr. Opin. Neurobiol.*, vol. 20, pp. 183–190, 2010.
- [56] G. Michalareas, J. Vezoli, S. van Pelt, J. M. Schoffelen, H. Kennedy, and P. Fries, “Alpha-beta and gamma rhythms subserve feedback and feedforward influences among human visual cortical areas,” *Neuron*, vol. 89, no. 2, pp. 384–397, 2016.
- [57] M. W. Self, T. van Kerkoerle, R. Goebel, and P. R. Roelfsema, “Benchmarking laminar fmri: Neuronal spiking and synaptic activity during top-down and bottom-up processing in the different layers of cortex,” *NeuroImage*, vol. 197, pp. 806–817, 2019.

- [58] L. Muckli and L. S. Petro, “Network interactions: non-geniculate input to v1,” *Current opinion in neurobiology*, vol. 23, no. 2, pp. 195–201, 2013.
- [59] E. P. Cook and J. H. Maunsell, “Attentional modulation of behavioral performance and neuronal responses in middle temporal and ventral intraparietal areas of macaque monkey,” *The Journal of neuroscience : the official journal of the Society for Neuroscience*, vol. 22, no. 5, pp. 1994–2004, 2002.
- [60] T. Z. Lauritzen, M. D’Esposito, D. J. Heeger, and M. A. Silver, “Top-down flow of visual spatial attention signals from parietal to occipital cortex,” *Journal of vision*, vol. 9, no. 13, pp. 1–14, 2009.
- [61] J. R. Cavanaugh, W. Bair, and J. A. Movshon, “Nature and interaction of signals from the receptive field center and surround in macaque v1 neurons,” *Journal of Neurophysiology*, vol. 88, no. 4, pp. 2530–2546, 2002a.
- [62] S. Shushruth, P. Mangapathy, J. M. Ichida, P. C. Bressloff, L. Schwabe, and A. Angelucci, “Strong recurrent networks compute the orientation tuning of surround modulation in the primate primary visual cortex,” *The Journal of Neuroscience*, vol. 32, pp. 308–321, 2012.
- [63] C. A. Henry, S. Joshi, D. Xing, R. M. Shapley, and M. J. Hawken, “Functional characterization of the extraclassical receptive field in macaque v1: contrast, orientation, and temporal dynamics,” *The Journal of neuroscience*, vol. 33, no. 14, pp. 6230–6242, 2013.
- [64] D. Tadin, J. S. Lappin, L. A. Gilroy, and R. Blake, “Perceptual consequences of centre- surround antagonism in visual motion processing,” *Nature*, vol. 424, pp. 312–315, 2003.
- [65] A. Angelucci, M. Bijanzadeh, L. Nurminen, F. Federer, S. Merlin, and P. C. Bressloff, “Circuits and mechanisms for surround modulation in visual cortex,” *Annual Review of Neuroscience*, vol. 40, pp. 425–451, 2017.
- [66] A. J. Parker and W. T. Newsome, “Sense and the single neuron: probing the physiology of perception,” *Annual review of neuroscience*, vol. 21, pp. 227–277, 1998.

- [67] G. Purushothaman and D. C. Bradley, “Neural population code for fine perceptual decisions in area mt,” *Nature neuroscience*, vol. 8, no. 1, pp. 99–106, 2005.
- [68] K. E. I. and K. M., “Center-surround organization of auditory receptive fields in the owl,” *Science*, vol. 202, pp. 778–780, 1978.
- [69] M. L. Sutter, C. E. Schreiner, M. McLean, K. N. O’connor, and W. C. Loftus, “Organization of inhibitory frequency receptive fields in cat primary auditory cortex,” *Journal of neurophysiology*, vol. 82, no. 5, pp. 2358–2371, 1999.
- [70] F. Vega-Bermudez and K. O. Johnson, “Surround suppression in the responses of primate sa1 and ra mechanoreceptive afferents mapped with a probe array,” *Journal of neurophysiology*, vol. 81, no. 6, pp. 2711–2719, 1999.
- [71] R. N. Sachdev, M. R. Krause, and J. A. Mazer, “Surround suppression and sparse coding in visual and barrel cortices. frontiers in neural circuits,” *Frontiers in neural circuits*, vol. 6, p. 43, 2012.
- [72] S. R. Olsen and R. I. Wilson, “Lateral presynaptic inhibition mediates gain control in an olfactory circuit,” *Nature*, vol. 452, no. 7190, pp. 956–960, 2008.
- [73] M. J. T., “Receptive fields of optic tract axons and lateral geniculate cells: Peripheral extent and barbiturate sensitivity,” *Journal of neurophysiology*, vol. 27, pp. 1154–1173, 1964.
- [74] S. G. Solomon, B. B. Lee, and H. Sun, “Suppressive surrounds and contrast gain in magnocellular-pathway retinal ganglion cells of macaque,” *The Journal of neuroscience*, vol. 26, no. 34, pp. 8715–8726, 2006.
- [75] P. Sterling and B. G. Wickelgren, “Visual receptive fields in the superior colliculus of the cat,” *Journal of neurophysiology*, vol. 32, no. 1, pp. 1–15, 1969.

- [76] M. E. Goldberg and R. H. Wurtz, "Activity of superior colliculus in behaving monkey. i. visual receptive fields of single neurons," *Journal of neurophysiology*, vol. 35, no. 4, pp. 542–559, 1972.
- [77] W. R. Levick, B. G. Cleland, and M. W. Dubin, "Lateral geniculate neurons of cat: retinal inputs and physiology," *Investigative ophthalmology*, vol. 11, no. 5, pp. 302–311, 1972.
- [78] R. T. Marrocco, J. W. McClurkin, and R. A. Young, "Modulation of lateral geniculate nucleus cell responsiveness by visual activation of the cortico-geniculate pathway," *The Journal of neuroscience*, vol. 2, no. 2, pp. 256–263, 1982.
- [79] S. G. Solomon, A. J. R. White, and P. R. Martin, "Extraclassical receptive field properties of parvocellular, magnocellular, and koniocellular cells in the primate lateral geniculate nucleus," *Journal of Neuroscience*, vol. 22, no. 1, pp. 338–349, 2002.
- [80] V. Bonin, V. Mante, and M. Carandini, "The suppressive field of neurons in lateral geniculate nucleus," *Journal of Neuroscience*, vol. 25, no. 47, pp. 10844–10856, 2005.
- [81] M. P. Sceniak, S. Chatterjee, and E. M. Callaway, "Visual spatial summation in macaque geniculocortical afferents," *Journal of Neurophysiology*, vol. 96, no. 6, pp. 3474–3484, 2006.
- [82] S. Shushruth, L. Nurminen, M. Bijanzadeh, J. M. Ichida, S. Vanni, and A. Angelucci, "Different orientation tuning of near- and far-surround suppression in macaque primary visual cortex mirrors their tuning in human perception," *The Journal of Neuroscience*, vol. 33, no. 1, pp. 106–119, 2013.
- [83] D. H. Hubel and T. N. Wiesel, "Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat," *Journal of Neurophysiology*, vol. 28, no. 2, pp. 229–289, 1965.
- [84] C. Blakemore and E. A. Tobin, "Lateral inhibition between orientation detectors in the cat's visual cortex," *Experimental brain research*, vol. 15, no. 4, pp. 439–440, 1972.

- [85] J. Nelson and B. Frost, "Orientation-selective inhibition from beyond the classic visual receptive field," *Brain Research*, vol. 139, no. 2, pp. 359–365, 1978.
- [86] M. P. Sceniak, M. J. Hawken, and R. Shapley, "Visual spatial characterization of macaque v1 neurons," *Journal of Neurophysiology*, vol. 85, no. 5, pp. 1873–1887, 2001.
- [87] G. Van den Bergh, B. Zhang, L. Arckens, and Y. M. Chino, "Receptive-field properties of v1 and v2 neurons in mice and macaque monkeys," *The Journal of comparative neurology*, vol. 518, no. 11, pp. 2051–2070, 2010.
- [88] J. Allman, F. Miezin, and E. McGuinness, "Stimulus specific responses from beyond the classical receptive field: neurophysiological mechanisms for local-global comparisons in visual neurons," *Annual review of neuroscience*, vol. 8, pp. 407–430, 1985.
- [89] R. Desimone and S. J. Schein, "Visual properties of neurons in area v4 of the macaque: sensitivity to stimulus form," *Journal of Neurophysiology*, vol. 57, no. 3, pp. 835–868, 1987.
- [90] R. T. Born and D. C. Bradley, "Structure and function of visual area mt," *Annual review of neuroscience*, vol. 28, pp. 157–189, 2005.
- [91] H. B. Barlow and W. A. Rosenblith, *Possible principles underlying the transformations of sensory messages*, pp. 217–234. MIT Press, 1961.
- [92] B. H. B., "Single units and sensation: a neuron doctrine for perceptual psychology?," *Perception*, vol. 1, no. 4, pp. 371–394, 1972.
- [93] W. E. Vinje and J. L. Gallant, "Sparse coding and decorrelation in primary visual cortex during natural vision," *Science*, vol. 287, no. 5456, pp. 1273–1276, 2000.
- [94] B. Haider, M. R. Krause, A. Duque, Y. Yu, J. Touryan, J. A. Mazer, and D. A. McCormick, "Synaptic and network mechanisms of sparse and reliable visual cortical activity during nonclassical receptive field stimulation," *Neuron*, vol. 65, no. 1, pp. 107–121, 2010.

- [95] M. Pecka, Y. Han, E. Sader, and T. D. Mrsic-Flogel, “Experience-dependent specialization of receptive field surround for selective coding of natural scenes,” *Neuron*, vol. 84, no. 2, pp. 457–469, 2014.
- [96] H. B. Turkozer, Z. Pamir, and H. Boyaci, “Contrast affects fmri activity in middle temporal cortex related to center-surround interaction in motion perception,” *Frontiers in Psychology*, vol. 7, pp. 1–8, 2016.
- [97] M.-P. Schallmo, A. M. Kale, A. V. Flevaris, Z. Brkanac, R. A. Edden, R. A. Bernier, and S. O. Murray, “Suppression and facilitation of human neural responses,” *eLife*, vol. 7, pp. 1–23, 2018.
- [98] M.-P. Schallmo, T. Kolodny, A. M. Kale, R. Millin, A. V. Flevaris, R. A. Edden, J. Gerds, R. A. Bernier, and S. O. Murray, “Weaker neural suppression in autism,” *Nature Communications*, vol. 11, p. 2675, 2020.
- [99] G. Er, Z. Pamir, and H. Boyaci, “Distinct patterns of surround modulation in v1 and hmt+,” *NeuroImage*, vol. 220, p. 117084, 2020.
- [100] D. Tadin, J. Kim, M. L. Doop, C. Gibson, J. S. Lappin, R. Blake, and S. Park, “Weakened center-surround interactions in visual motion processing in schizophrenia,” *Journal of Neuroscience*, vol. 26, no. 44, pp. 11403–11412, 2006.
- [101] D. Tadin, J. Silvanto, A. Pascual-Leone, and L. Battelli, “Improved motion perception and impaired spatial suppression following disruption of cortical area mt/v5,” *Journal of Neuroscience*, vol. 31, no. 4, pp. 1279–1283, 2011.
- [102] J. H. Foss-Feig, D. Tadin, K. B. Schauder, and C. J. Cascio, “A substantial and unexpected enhancement of motion perception in autism,” *The Journal of Neuroscience*, vol. 33, no. 19, pp. 8243–8249, 2013.
- [103] J. M. Ichida, L. Schwabe, P. C. Bressloff, and A. Angelucci, “Response facilitation from the “suppressive” receptive field surround of macaque v1 neurons,” *Journal of Neurophysiology*, vol. 98, no. 4, pp. 2168–2181, 2007.

- [104] J. R. Cavanaugh, W. Bair, and J. A. Movshon, "Selectivity and spatial distribution of signals from the receptive field surround in macaque v1 neurons," *Journal of Neurophysiology*, vol. 88, pp. 2547–2556, 2002b.
- [105] L. Schwabe, J. M. Ichida, S. Shushruth, P. Mangapathy, and A. Angelucci, "Contrast-dependence of surround suppression in macaque v1: Experimental testing of a recurrent network model," *NeuroImage*, vol. 52, no. 3, pp. 777–792, 2010. Computational Models of the Brain.
- [106] A. Angelucci, J. B. Levitt, E. J. Walton, J. M. Hupe, J. Bullier, and J. S. Lund, "Circuits for local and global signal integration in primary visual cortex," *The Journal of neuroscience : the official journal of the Society for Neuroscience*, vol. 22, no. 19, pp. 8633–8646, 2002.
- [107] J. Levitt and J. Lund, "The spatial extent over which neurons in macaque striate cortex pool visual signals," *Vis. Neurosci.*, vol. 19, pp. 439–452, 2002.
- [108] J. Ichida, L. Schwabe, P. Bressloff, and A. Angelucci, "Feedback-mediated facilitation and suppression from the receptive field surround of macaque v1 neurons," *Soc. Neurosci. Abstr. Online*, 2005. Program No. 820.4.
- [109] G. C. DeAngelis, R. D. Freeman, and I. Ohzawa, "Length and width tuning of neurons in the cat's primary visual cortex," *Journal of Neurophysiology*, vol. 71, no. 1, pp. 347–374, 1994.
- [110] G. A. Walker, I. Ohzawa, and R. D. Freeman, "Suppression outside the classical cortical receptive field," *Visual neuroscience*, vol. 17, no. 3, pp. 369–379, 2000.
- [111] J. B. Levitt and J. S. Lund, "Contrast dependence of contextual effects in primate visual cortex," *Nature*, vol. 387, no. 6628, pp. 73–76, 1997.
- [112] F. Sengpiel, A. Sen, and C. Blakemore, "Characteristics of surround inhibition in cat area 17," *Experimental brain research*, vol. 116, no. 2, pp. 216–228, 1997.

- [113] O. Sadakane, H. Ozeki, T. Naito, T. Akasaki, T. Kasamatsu, and H. Sato, "Contrast-dependent, contextual response modulation in primary visual cortex and lateral geniculate nucleus of the cat," *The European journal of neuroscience*, vol. 23, no. 6, pp. 1633–1642, 2006.
- [114] M. Sceniak, D. Ringach, M. Hawken, and R. Shapley, "Contrast's effect on spatial summation by macaque v1 neurons," *Nature neuroscience*, vol. 2, pp. 733–9, 1999.
- [115] U. Polat, K. Mizobe, M. W. Pettet, T. Kasamatsu, and A. M. Norcia, "Collinear stimuli regulate visual responses depending on cell's contrast threshold," *Nature*, vol. 391, no. 6667, pp. 580–584, 1998.
- [116] G. A. Walker, I. Ohzawa, and R. D. Freeman, "Asymmetric suppression outside the classical receptive field of the visual cortex," *Journal of Neuroscience*, vol. 19, no. 23, pp. 10536–10553, 1999.
- [117] C. C. Pack, J. N. Hunter, and R. T. Born, "Contrast dependence of suppressive influences in cortical area mt of alert macaque," *Journal of Neurophysiology*, vol. 93, no. 3, pp. 1809–1815, 2005.
- [118] B. G. Breitmeyer, H. Kafaligönül, H. Öğmen, L. Mardon, S. Todd, and R. Ziegler, "Meta-and paracontrast reveal differences between contour- and brightness-processing mechanisms," *Vision research*, vol. 46, no. 17, pp. 2645–2658, 2006.
- [119] V. Di Lollo, J. T. Enns, and R. A. Rensink, "Competition for consciousness among visual events: the psychophysics of reentrant visual processes," *Journal of Experimental Psychology: General*, vol. 129, no. 4, p. 481, 2000.
- [120] H. Kafaligönül, B. G. Breitmeyer, and H. Öğmen, "Effects of contrast polarity in paracontrast masking," *Attention, Perception, & Psychophysics*, vol. 71, no. 7, pp. 1576–1587, 2009.
- [121] S. J. Joo, G. M. Boynton, and S. O. Murray, "Long-range, pattern-dependent contextual effects in early human visual cortex," *Current biology : CB*, vol. 22, no. 9, pp. 781–786, 2012.

- [122] A. V. Flevaris and S. O. Murray, “Feature-based attention modulates surround suppression,” *Journal of Vision*, vol. 15, no. 1, pp. 1–11, 2015.
- [123] A. V. Flevaris and S. O. Murray, “Attention determines contextual enhancement versus suppression in human primary visual cortex,” *The Journal of Neuroscience*, vol. 35, no. 35, pp. 12273–12280, 2015.
- [124] B. Zenger-Landolt and D. J. Heeger, “Response suppression in v1 agrees with psychophysics of surround masking,” *Journal of Neuroscience*, vol. 23, no. 17, pp. 6884–6893, 2003.
- [125] A. L. Williams, K. D. Singh, and A. T. Smith, “Surround modulation measured with functional mri in the human visual cortex,” *Journal of Neurophysiology*, vol. 89, no. 1, pp. 525–533, 2003.
- [126] M. Pihlaja, L. Henriksson, A. James, and S. Vanni, “Quantitative multifocal fmri shows active suppression in human v1,” *Human Brain Mapping*, vol. 29, no. 9, pp. 1001–1014, 2008.
- [127] C. C. Chen, T. Kasamatsu, U. Polat, and A. M. Norcia, “Contrast response characteristics of long-range lateral interactions in cat striate cortex,” *Neuroreport*, vol. 12, no. 4, pp. 655–661, 2001.
- [128] G. M. Boynton, J. B. Demb, G. H. Glover, and D. J. Heeger, “Neuronal basis of contrast discrimination,” *Vision Research*, vol. 39, no. 2, pp. 257–269, 1999.
- [129] F. Sengpiel and V. Vorobyov, “Intracortical origins of interocular suppression in the visual cortex,” *Journal of Neuroscience*, vol. 25, no. 27, pp. 6394–6400, 2005.
- [130] L. Schwabe, K. Obermayer, A. Angelucci, and P. C. Bressloff, “The role of feedback in shaping the extra-classical receptive field of cortical neurons: a recurrent network model,” *Journal of Neuroscience*, vol. 26, no. 36, pp. 9117–9129, 2006.

- [131] M. Ito and C. D. Gilbert, “Attention modulates contextual influences in the primary visual cortex of alert monkeys,” *Neuron*, vol. 22, pp. 593–604, 1999.
- [132] M. P. Schallmo, A. M. Kale, and S. O. Murray, “The time course of different surround suppression mechanisms,” *Journal of vision*, vol. 19, no. 4, p. 12, 2019.
- [133] J.-D. Haynes, G. Roth, M. Stadler, and H.-J. Heinze, “Neuromagnetic correlates of perceived contrast in primary visual cortex,” *Journal of Neurophysiology*, vol. 89, no. 5, pp. 2655–2666, 2003.
- [134] S. J. Joo and S. O. Murray, “Contextual effects in human visual cortex depend on surface structure,” *Journal of Neurophysiology*, vol. 111, no. 9, pp. 1783–1791, 2014.
- [135] Y. Ohtani, S. Okamura, Y. Yoshida, K. Toyama, and Y. Ejima, “Surround suppression in the human visual cortex: an analysis using magnetoencephalography,” *Vision research*, vol. 42, no. 15, pp. 1825–1835, 2002.
- [136] M. I. Vanegas, A. Blangero, and S. P. Kelly, “Electrophysiological indices of surround suppression in humans,” *Journal of neurophysiology*, vol. 113, no. 4, pp. 1100–1109, 2015.
- [137] D. Tadin, “Suppressive mechanisms in visual motion processing: From perception to intelligence,” *Vision Research*, vol. 115, pp. 58–70, 2015.
- [138] D. Tadin, W. Park, K. Dieter, M. D. Melnick, J. S. Lappin, and B. R., “Spatial suppression promotes rapid figure-ground segmentation of moving objects,” *Nature Communications*, vol. 10, p. 2732, 2019.
- [139] D. Tadin, C. L. E. Paffen, R. Blake, and J. S. Lappin, “Contextual modulations of center-surround interactions in motion revealed with the motion aftereffect,” *Journal of Vision*, vol. 8, no. 7, pp. 1–11, 2008.
- [140] L. Nurminen, M. Kilpeläinen, and S. Vanni, “Fovea-periphery axis symmetry of surround modulation in the human visual system,” *PLOS ONE*, vol. 8, no. 2, pp. 1–11, 2013.

- [141] L. Nurminen, M. Kilpeläinen, P. Laurinen, and S. Vanni, “Area summation in human visual system: Psychophysics, fmri, and modeling,” *Journal of Neurophysiology*, vol. 102, no. 5, pp. 2900–2909, 2009.
- [142] J. D. Golomb, J. R. B. McDavitt, B. M. Ruf, J. I. Chen, A. Saricicek, K. H. Maloney, J. Hu, M. M. Chun, and Z. Bhagwagar, “Enhanced visual motion perception in major depressive disorder,” *Journal of Neuroscience*, vol. 29, no. 28, pp. 9072–9077, 2009.
- [143] O. V. Sysoeva, I. A. Galuta, M. S. Davletshina, E. V. Orekhova, and T. A. Stroganova, “Abnormal size-dependent modulation of motion perception in children with autism spectrum disorder (asd),” *Frontiers in Neuroscience*, vol. 11, p. 164, 2017.
- [144] A. Rosenberg, J. S. Patterson, and D. E. Angelaki, “A computational perspective on autism,” *Proceedings of the National Academy of Sciences*, vol. 112, no. 30, pp. 9158–9165, 2015.
- [145] Z. X., C. Y., Z. X., X. T., C. T., J. G., and Y. X., “Impaired center-surround suppression in patients with alzheimer’s disease,” *Journal of Alzheimer’s Disease*, vol. 55, pp. 1101–1108, 2017.
- [146] J. Battista, D. R. Badcock, and A. M. McKendrick, “Center-Surround Visual Motion Processing in Migraine,” *Investigative ophthalmology & visual science*, vol. 51, no. 11, pp. 6070–6076, 2010.
- [147] P. Yazdani, J. C. Read, R. G. Whittaker, and A. J. Trevelyan, “Assessment of epilepsy using noninvasive visual psychophysics tests of surround suppression,” *Physiological Reports*, vol. 5, no. 5, p. e13079, 2017.
- [148] L. R. Betts, C. P. Taylor, A. B. Sekuler, and P. J. Bennett, “Aging reduces center-surround antagonism in visual motion processing,” *Neuron*, vol. 45, no. 3, pp. 361–366, 2005.
- [149] A. G. Leventhal, Y. Wang, M. Pu, Y. Zhou, and Y. Ma, “Gaba and its agonists improved visual cortical function in senescent monkeys,” *Science*, vol. 300, no. 5620, pp. 812–815, 2003.

- [150] J. H. Yoon, R. J. Maddock, A. Rokem, M. A. Silver, M. J. Minzenberg, J. D. Ragland, and C. S. Carter, “Gaba concentration is reduced in visual cortex in schizophrenia and correlates with orientation-specific surround suppression,” *Journal of Neuroscience*, vol. 30, no. 10, pp. 3777–3781, 2010.
- [151] A. Wassef, J. Baker, and L. D. Kochan, “Gaba and schizophrenia: a review of basic science and clinical studies,” *Journal of clinical psychopharmacology*, vol. 23, no. 6, pp. 601–640, 2003.
- [152] M. D. Melnick, B. R. Harrison, S. Park, L. Bennetto, and D. Tadin, “A strong interactive link between sensory discriminations and intelligence,” *Current biology*, vol. 23, no. 11, pp. 1013–1017, 2013.
- [153] S. O. Murray, M. P. Schallmo, T. Kolodny, R. Millin, A. Kale, R. Thomas, P., T. T. H., R. A. S. J., Bernier, and D. Tadin, “Sex differences in visual motion processing,” *Current Biology*, vol. 28, no. 17, pp. 2794–2799, 2018.
- [154] M. M. Chun, J. D. Golomb, and N. B. Turk-Browne, “A taxonomy of external and internal attention,” *Annual Review of Psychology*, vol. 62, no. 1, pp. 73–101, 2011.
- [155] S. K. Ungerleider and L. G., “Mechanisms of visual attention in the human cortex,” *Annual Review of Neuroscience*, vol. 23, no. 1, pp. 315–341, 2000.
- [156] R. Desimone, J. Duncan, *et al.*, “Neural mechanisms of selective visual attention,” *Annual review of neuroscience*, vol. 18, no. 1, pp. 193–222, 1995.
- [157] M. I. Posner, “Orienting of attention,” *Quarterly journal of experimental psychology*, vol. 32, no. 1, pp. 3–25, 1980.
- [158] C. W. Eriksen and Y.-y. Yeh, “Allocation of attention in the visual field.,” *Journal of Experimental Psychology: Human Perception and Performance*, vol. 11, no. 5, p. 583, 1985.
- [159] U. Castiello and C. Umiltà, “Size of the attentional focus and efficiency of processing,” *Acta Psychologica*, vol. 73, pp. 195–209, 4 1990.

- [160] J. M. Henderson and A. D. Macquistan, “The spatial distribution of attention following an exogenous cue,” *Perception & Psychophysics* 1993 53:2, vol. 53, pp. 221–230, 3 1993.
- [161] D. LaBerge, R. L. Carlson, J. K. Williams, and B. G. Bunney, “Shifting attention in visual space: Tests of moving-spotlight models versus an activity-distribution model,” *Journal of Experimental Psychology: Human Perception and Performance*, vol. 23, no. 5, p. 1380, 1997.
- [162] K. R. Cave and J. M. Zimmerman, “Flexibility in spatial attention before and after practice,” *Psychological Science*, vol. 8, no. 5, pp. 399–403, 1997.
- [163] D. O. Bahcall and E. Kowler, “Attentional interference at small spatial separations,” *Vision Research*, vol. 39, pp. 71–86, 1 1999.
- [164] J. H. Fecteau and J. T. Enns, “Visual letter matching: Hemispheric functioning or scanning biases?,” *Neuropsychologia*, vol. 43, pp. 1412–1428, 1 2005.
- [165] J. S. McCarley and J. R. Mounts, “Localized attentional interference affects object individuation, not feature detection,” *Perception*, vol. 36, pp. 17–32, 6 2007.
- [166] N. G. Müller, M. Mollenhauer, A. Rösler, and A. Kleinschmidt, “The attentional field has a mexican hat distribution,” *Vision research*, vol. 45, no. 9, pp. 1129–1137, 2005.
- [167] J. R. Mounts, “Attentional capture by abrupt onsets and feature singletons produces inhibitory surrounds,” *Perception & Psychophysics* 2000 62:7, vol. 62, pp. 1485–1493, 2000.
- [168] G. Caputo and S. Guerra, “Attentional selection by distractor suppression,” *Vision Research*, vol. 38, pp. 669–689, 3 1998.
- [169] L. Heinemann, A. Kleinschmidt, and N. G. Müller, “Exploring bold changes during spatial attention in non-stimulated visual cortex,” *PLOS ONE*, vol. 4, p. e5560, 5 2009.

- [170] J. M. Hopf, C. N. Boehler, M. A. Schoenfeld, H. J. Heinze, and J. K. Tsotsos, “The spatial profile of the focus of attention in visual search: Insights from meg recordings,” *Vision Research*, vol. 50, pp. 1312–1320, 6 2010.
- [171] N. G. Müller and A. Kleinschmidt, “The attentional ‘spotlight’s’ penumbra: center-surround modulation in striate cortex,” *Neuroreport*, vol. 15, no. 6, pp. 977–980, 2004.
- [172] C. N. Boehler, T. F. Münte, R. M. Krebs, H. J. Heinze, M. A. Schoenfeld, and J. M. Hopf, “Sensory meg responses predict successful and failed inhibition in a stop-signal task,” *Cerebral Cortex*, vol. 19, pp. 134–145, 1 2009.
- [173] C. N. Boehler, J. K. Tsotsos, M. A. Schoenfeld, H. J. Heinze, and J. M. Hopf, “Neural mechanisms of surround attenuation and distractor competition in visual search,” *Journal of Neuroscience*, vol. 31, pp. 5213–5224, 4 2011.
- [174] J. M. Hopf, C. N. Boehler, S. J. Luck, J. K. Tsotsos, H. J. Heinze, and M. A. Schoenfeld, “Direct neurophysiological evidence for spatial suppression surrounding the focus of attention in vision,” *Proceedings of the National Academy of Sciences*, vol. 103, pp. 1053–1058, 1 2006.
- [175] J. H. R. Maunsell, “Neuronal mechanisms of visual attention,” *Annual Review of Vision Science*, vol. 1, pp. 373–391, 2015.
- [176] J. Moran and R. Desimone, “Selective attention gates visual processing in the extrastriate cortex,” *Science*, vol. 229, pp. 782–784, 1985.
- [177] S. J. Luck, L. Chelazzi, S. A. Hillyard, and R. Desimone, “Neural mechanisms of spatial selective attention in areas v1, v2, and v4 of macaque visual cortex,” *Journal of Neurophysiology*, vol. 77, pp. 24–42, 1997.
- [178] J. H. Reynolds and R. Desimone, “The role of neural mechanisms of attention in solving the binding problem,” *Neuron*, vol. 24, pp. 19–29, 9 1999.

- [179] J. Lee and J. H. R. Maunsell, "Attentional modulation of mt neurons with single or multiple stimuli in their receptive fields," *Journal of Neuroscience*, vol. 30, no. 8, pp. 3058–3066, 2010.
- [180] G. M. Ghose and J. H. R. Maunsell, "Spatial summation can explain the attentional modulation of neuronal responses to multiple stimuli in area v4," *Journal of Neuroscience*, vol. 28, no. 19, pp. 5115–5126, 2008.
- [181] A. M. Ni, S. Ray, and J. H. Maunsell, "Tuned normalization explains the size of attention modulations," *Neuron*, vol. 73, no. 4, pp. 803–813, 2012.
- [182] S. Treue and J. H. Maunsell, "Attentional modulation of visual motion processing in cortical areas mt and mst," *Nature*, vol. 382, no. 6591, pp. 539–541, 1996.
- [183] K. A. Sundberg, J. F. Mitchell, and J. H. Reynolds, "Spatial attention modulates center-surround interactions in macaque visual area v4," *Neuron*, vol. 61, no. 6, pp. 952–963, 2009.
- [184] J. Duncan and G. W. Humphreys, "Visual search and stimulus similarity.," *Psychological review*, vol. 96, no. 3, p. 433, 1989.
- [185] C. J. McAdams and J. H. Maunsell, "Effects of attention on orientation-tuning functions of single neurons in macaque cortical area v4," *Journal of Neuroscience*, vol. 19, no. 1, pp. 431–441, 1999.
- [186] J. H. Reynolds and L. Chelazzi, "Attentional modulation of visual processing," *Annual Review of Neuroscience*, vol. 27, no. 1, pp. 611–647, 2004.
- [187] J. H. Reynolds, T. Pasternak, and R. Desimone, "Attention increases sensitivity of v4 neurons," *Neuron*, vol. 26, pp. 703–714, 6 2000.
- [188] J. H. Reynolds and R. Desimone, "Interacting roles of attention and visual salience in v4," *Neuron*, vol. 37, pp. 853–863, 3 2003.
- [189] M. Carrasco and S. Ling, "Attention alters appearance," *Nature Neuroscience*, vol. 7, no. 3, pp. 308–313, 2004.

- [190] M. Carrasco, “Visual attention: The past 25 years,” *Vision Research*, vol. 51, no. 13, pp. 1484–1525, 2011.
- [191] M. Carrasco, “How visual spatial attention alters perception,” *Cognitive Processing*, vol. 19, no. Suppl 1, pp. 77–88, 2018.
- [192] E. K. Cutrone, D. J. Heeger, and M. Carrasco, “Attention enhances contrast appearance via increased input baseline of neural responses,” *Journal of vision*, vol. 14, no. 14, p. 16, 2014.
- [193] J. C. Martinez-Trujillo and S. Treue, “Attentional modulation strength in cortical area mt depends on stimulus contrast,” *Neuron*, vol. 35, p. 2, 2002.
- [194] T. Williford and J. H. Maunsell, “Effects of spatial attention on contrast response functions in macaque area v4,” *Journal of Neurophysiology*, vol. 96, pp. 40–54, 2006.
- [195] S. Treue and J. C. M. Trujillo, “Feature-based attention influences motion processing gain in macaque visual cortex,” *Nature*, vol. 399, no. 6736, pp. 575–579, 1999.
- [196] J. C. Martinez-Trujillo and S. Treue, “Feature-based attention increases the selectivity of population responses in primate visual cortex,” *Current biology*, vol. 14, no. 9, pp. 744–751, 2004.
- [197] E. Seidemann and W. T. Newsome, “Effect of spatial attention on the responses of area mt neurons,” *Journal of Neurophysiology*, vol. 81, no. 4, pp. 1783–1794, 1999.
- [198] D. J. Heeger, “Normalization of cell responses in cat striate cortex,” *Visual Neuroscience*, vol. 9, no. 2, pp. 181–197, 1992.
- [199] M. Carandini and D. J. Heeger, “Normalization as a canonical neural computation,” *Nature Reviews Neuroscience*, vol. 13, no. 1, pp. 51–62, 2012.
- [200] D. G. Albrecht and D. B. Hamilton, “Striate cortex of monkey and cat: contrast response function.,” *Journal of Neurophysiology*, vol. 48, no. 1, pp. 217–237, 1982.

- [201] M. Carandini, D. J. Heeger, and J. A. Movshon, “Linearity and normalization in simple cells of the macaque primary visual cortex,” *Journal of Neuroscience*, vol. 17, no. 21, pp. 8621–8644, 1997.
- [202] J. Lee and J. H. R. Maunsell, “The effect of attention on neuronal responses to high and low contrast stimuli,” *Journal of Neurophysiology*, vol. 104, pp. 960–971, 2010.
- [203] X. Li and M. Basso, “Preparing to move increases the sensitivity of superior colliculus neurons,” *The Journal of neuroscience : the official journal of the Society for Neuroscience*, vol. 28, pp. 4561–77, 2008.
- [204] S. Itthipuripat, J. O. Garcia, N. Rungratsameetaweemana, T. C. Sprague, and J. T. Serences, “Changing the spatial scope of attention alters patterns of neural gain in human cortex,” *Journal of Neuroscience*, vol. 34, no. 1, pp. 112–123, 2014.
- [205] G. M. Boynton, “A framework for describing the effects of attention on visual responses,” *Vision research*, vol. 49, no. 10, pp. 1129–1143, 2009.
- [206] G. M. Ghose and I. T. Harrison, “Temporal precision of neuronal information in a rapid perceptual judgment,” *Journal of Neurophysiology*, vol. 101, no. 3, pp. 1480–1493, 2009.
- [207] J. Lee and J. H. Maunsell, “A normalization model of attentional modulation of single unit responses,” *PloS one*, vol. 4, no. 2, p. e4651, 2009.
- [208] M. Roberts, L. S. Delicato, J. Herrero, M. A. Gieselmann, and A. Thiele, “Attention alters spatial integration in macaque v1 in an eccentricity-dependent manner,” *Nature Neuroscience*, vol. 10, pp. 1483–1491, 2007.
- [209] E. Freeman, D. Sagi, and J. Driver, “Lateral interactions between targets and flankers in low-level vision depend on attention to the flankers,” *Nature Neuroscience*, vol. 4, pp. 1032–1036, 2001.
- [210] B. C. Motter, “Focal attention produces spatially selective processing in visual cortical areas v1, v2, and v4 in the presence of competing stimuli,” *Journal of Neurophysiology*, vol. 70, no. 3, pp. 909–919, 1993.

- [211] K. Anton-Erxleben, V. M. Stephan, and S. Treue, “Attention reshapes center-surround receptive field structure in macaque cortical area mt,” *Cerebral Cortex*, vol. 19, pp. 2466—478, 2009.
- [212] T. Womelsdorf, K. Anton-Erxleben, F. Pieper, and S. Treue, “Dynamic shifts of visual receptive fields in cortical area mt by spatial attention,” *Nature Neuroscience*, vol. 9, pp. 1156–1160, 2006.
- [213] B. Liu, X. Wang, L. Wang, Q. Qu, W. Zhang, B. Wang, J. Xiang, T. Yan, T. Yan, and H. Zhang, “Attention field size alters patterns of population receptive fields in the early visual cortex,” *Neuroscience bulletin*, vol. 38, no. 2, pp. 205–208, 2022.
- [214] J. Poort, F. Raudies, A. Wannig, V. A. Lamme, H. Neumann, and P. R. Roelfsema, “The role of attention in figure-ground segregation in areas v1 and v4 of the visual cortex,” *Neuron*, vol. 75, no. 1, pp. 143–156, 2012.
- [215] J. Poort, M. W. Self, B. van Vugt, H. Malkki, and P. R. Roelfsema, “Texture segregation causes early figure enhancement and later ground suppression in areas v1 and v4 of visual cortex,” *Cerebral cortex (New York, N.Y. : 1991)*, vol. 26, no. 10, pp. 3964–3976, 2016.
- [216] P. R. Roelfsema and F. P. de Lange, “Early visual cortex as a multiscale cognitive blackboard,” *Annual review of vision science*, vol. 2, pp. 131–151, 2016.
- [217] R. Coen-Cagli, A. Kohn, and O. Schwartz, “Flexible gating of contextual influences in natural vision,” *Nature Neuroscience*, vol. 18, pp. 1648–1655, 2015.
- [218] W. E. Vinje and J. L. Gallant, “Sparse coding and decorrelation in primary visual cortex during natural vision,” *Science*, vol. 287, pp. 1273–1276, 2000.
- [219] B. Borghuis, D. Tadin, M. Lankheet, J. Lappin, and W. van de Grind, “Temporal limits of visual motion processing: Psychophysics and neurophysiology,” *Vision*, vol. 3, no. 1, p. 5, 2019.

- [220] F. A. A. Kingdom and N. Prins, *Psychophysics: A Practical Introduction*. London: Academic Press: an imprint of Elsevier, 2010.
- [221] R. T. Born and R. B. H. Tootell, “Segregation of global and local motion processing in primate middle temporal visual area,” *Nature*, vol. 357, p. 497–499, 1992.
- [222] V. A. F. Lamme, “The neurophysiology of figure-ground segregation in primary visual cortex,” *Journal of Neuroscience*, vol. 15, pp. 1605–1616, 1995.
- [223] S. Kastner, H. C. Nothdurft, and I. N. Pigarev, “Neuronal correlates of pop-out in cat striate cortex,” *Vision Research*, vol. 37, pp. 371–376, 1995.
- [224] T. Williford and J. H. Maunsell, “Effects of spatial attention on contrast response functions in macaque area v4,” *Journal of Neurophysiology*, vol. 96, no. 1, pp. 40–54, 2006.
- [225] K. A. Sundberg, J. F. Mitchell, and J. H. Reynolds, “Attention influences single unit and local field potential response latencies in visual cortical area v4,” *The Journal of Neuroscience*, vol. 32, no. 45, pp. 16040–16050, 2012.
- [226] C. Moutsiana, D. T. Field, and J. P. Harris, “The neural basis of centre-surround interactions in visual motion processing,” *PLoS ONE*, vol. 6, no. 7, p. e22902, 2011.
- [227] C. L. E. Paffen, D. Alais, and F. A. Verstraten, “Center-surround inhibition deepens binocular rivalry suppression,” *Vision Research*, vol. 45, pp. 2642–2649, 2005a.
- [228] C. L. E. Paffen, J. van der Smagt, Maarten, S. te Pas, and F. Verstraten, “Center-surround inhibition and facilitation as a function of size and contrast at multiple levels of visual motion processing,” *Journal of Vision*, vol. 5, pp. 571–578, 2005b.
- [229] M. Kiniklioglu and H. Boyaci, “Increasing the spatial extent of attention strengthens surround suppression,” *Vision Research*, vol. 199, p. 108074, 2022.

- [230] A. C. Huk, R. F. Dougherty, and D. J. Heeger, “Retinotopy and functional subdivision of human areas mt and mst,” *Journal of Neuroscience*, vol. 22, no. 5, pp. 7195–7205, 2002.
- [231] S. A. Engel, G. H. Glover, and B. A. Wandell, “Retinotopic organization in human visual cortex and the spatial precision of functional mri,” *Cerebral Cortex*, vol. 7, no. 2, pp. 181–192, 1997.
- [232] M. I. Sereno, A. M. Dale, J. B. Reppas, K. Kwong, J. W. Belliveau, T. J. Brady, B. R. Rosen, and R. B. Tootell, “Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging,” *Science*, vol. 268, no. 5212, pp. 889–893, 1995.
- [233] A. S. Greenberg, T. Verstynen, Y.-C. Chiu, S. Yantis, W. Schneider, and M. Behrmann, “Visuotopic cortical connectivity underlying attention revealed with white-matter tractography,” *Journal of Neuroscience*, vol. 32, no. 8, pp. 2773–2782, 2012.
- [234] S. D. Slotnick and S. Yantis, “Efficient acquisition of human retinotopic maps,” *Human Brain Mapping*, vol. 18, no. 1, pp. 22–29, 2003.
- [235] A. M. Dale, B. Fischl, and M. I. Sereno, “Cortical surface-based analysis: I. segmentation and surface reconstruction,” *NeuroImage*, vol. 9, no. 2, pp. 179–194, 1999.
- [236] B. Fischl, M. I. Sereno, and A. M. Dale, “Cortical surface-based analysis: Ii: Inflation, flattening, and a surface-based coordinate system,” *NeuroImage*, vol. 9, no. 2, pp. 195–207, 1999.
- [237] M. W. Woolrich, B. D. Ripley, M. Brady, and S. M. Smith, “Temporal autocorrelation in univariate linear modeling of fmri data,” *NeuroImage*, vol. 14, no. 6, pp. 1370–1386, 2001.
- [238] M. Jenkinson, C. F. Beckmann, T. E. Behrens, M. W. Woolrich, and S. M. Smith, “Fsl,” *NeuroImage*, vol. 62, no. 2, pp. 782–790, 2012.
- [239] S. M. Smith, M. Jenkinson, M. W. Woolrich, C. F. Beckmann, T. E. Behrens, H. Johansen-Berg, P. R. Bannister, M. De Luca, I. Drobnjak,

- D. E. Flitney, R. K. Niazy, J. Saunders, J. Vickers, Y. Zhang, N. De Stefano, J. M. Brady, and P. M. Matthews, “Advances in functional and structural mr image analysis and implementation as fsl,” *NeuroImage*, vol. 23, no. 2, pp. S208–S219, 2004.
- [240] C. M. Stoppel, C. N. Boehler, H. Strumpf, H. J. Heinze, T. Noesselt, J. M. Hopf, and M. A. Schoenfeld, “Feature-based attention modulates direction-selective hemodynamic activity within human mt,” *Human brain mapping*, vol. 32, no. 12, pp. 2183–2192, 2011.
- [241] C. Büchel, O. Josephs, G. Rees, R. Turner, C. D. Frith, and K. J. Friston, “The functional anatomy of attention to visual motion. a functional mri study,” *Brain : a journal of neurology*, vol. 121, no. 7, pp. 1281–1294, 1998.
- [242] L. Muckli and L. S. Petro, “Network interactions: non-geniculate input to v1,” *Current Opinion in Neurobiology*, vol. 23, no. 2, pp. 195–201, 2013.
- [243] B. J., “Integrated model of visual processing,” *Brain research reviews*, vol. 36, no. 2, pp. 96–107, 2001.
- [244] H. Takemura, H. Ashida, K. Amano, A. Kitaoka, and I. Murakami, “Neural correlates of induced motion perception in the human brain,” *The Journal of neuroscience : the official journal of the Society for Neuroscience*, vol. 32, no. 41, pp. 14344–14354, 2012.
- [245] L. Liu, R. Haefner, and C. Pack, “A neural basis for the spatial suppression of visual motion perception,” *eLife*, vol. 5, p. e16167, 2016.
- [246] T. Liu, J. Abrams, and M. Carrasco, “Voluntary attention enhances contrast appearance,” *Psychological Science*, vol. 20, no. 3, pp. 354–362, 2009.
- [247] Y. Petrov, M. Carandini, and S. McKee, “Two distinct mechanisms of suppression in human vision,” *Journal of Neuroscience*, vol. 25, no. 38, pp. 8704–8707, 2005.
- [248] J. Xing and D. J. Heeger, “Measurement and modeling of center-surround suppression and enhancement,” *Vision Research*, vol. 41, pp. 571–583, 2001.

- [249] I. C. Clayton, J. C. Richards, and C. J. Edwards, “Selective attention in obsessive-compulsive disorder,” *Journal of Abnormal Psychology*, vol. 108, no. 1, pp. 171–175, 1999.
- [250] Y. Habermann-Paelecke, J. Pohl, and B. Leplow, “Attention and executive functions in remitted major depression patients,” *Journal of Affective Disorders*, vol. 89, no. 1-3, pp. 125–135, 2005.
- [251] S. J. Luck and J. M. Gold, “The construct of attention in schizophrenia,” *Biological Psychiatry*, vol. 64, no. 1, pp. 34–39, 2008.
- [252] J. Kreither, J. Lopez-Calderon, C. J. Leonard, B. M. Robinson, A. Ruffle, B. Hahn, J. M. Gold, and S. J. Luck, “Electrophysiological evidence for hyperfocusing of spatial attention in schizophrenia,” *Journal of Neuroscience*, vol. 37, no. 14, pp. 3813–3823, 2017.
- [253] A. Kosovicheva, S. Sheremata, A. Rokem, A. Landau, and M. Silver, “Cholinergic enhancement reduces orientation-specific surround suppression but not visual crowding,” *Frontiers in Behavioral Neuroscience*, vol. 6, 2012.
- [254] S. Poltoratski, S. Ling, D. McCormack, and F. Tong, “Characterizing the effects of feature salience and top-down attention in the early visual system,” *Journal of neurophysiology*, vol. 118, no. 1, pp. 564—573, 2017.
- [255] M.-P. Schallmo, A. N. Grant, P. C. Burton, and C. A. Olman, “The effects of orientation and attention during surround suppression of small image features: A 7 tesla fmri study,” *Journal of Vision*, vol. 16, no. 10, p. 19, 2016.