

CHARACTERIZING SURROUND SUPPRESSION IN MOTION DIRECTION PERCEPTION

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CHARACTERIZING SURROUND SUPPRESSION IN MOTION
DIRECTION PERCEPTION

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

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ABSTRACT

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Visual perception is often achieved by surround modulation mechanisms, which help us pool individual information in our visual field. This mechanism is also prominent in motion perception, namely motion discrimination. A center-surround antagonistic organization aids motion perception using these modulation mechanisms, which are facilitation or suppression. Decisions to which modulation type will take place are usually manipulated by changing size and contrast of drifting Gabor disc stimuli. Because a systematic investigation of these mechanisms is not conducted in prior research, we have used three different types of stimulus (small disc, annular, and large disc grating) to see whether there is a facilitative or suppressive pattern between duration thresholds of these stimuli. To achieve this, we performed a behavioral study, that would assess motion discrimination thresholds of human participants for these stimuli via adaptive staircase procedures. Then, we looked for three possible pooling regimes by comparing duration thresholds of small disc-annular-large disc grating stimulus sets: efficient or inefficient (weak or strong suppression) pooling. We found that duration thresholds of large disc gratings were almost greater than small disc or annular gratings almost all the time in both contrast levels, which indicated a strong suppression. We have also conducted simulations of divisive normalization models and observed that modulation mechanisms were more prominent in simulated duration thresholds using MT parameters from literature than V1. Although previous literature suggests that MT region produces facilitative or suppressive effects within itself, we are not able to postulate a specific brain region creating strong suppressive pooling we observed in our behavioral data. This is why this study is a critical next step for future neuroimaging studies.

Keywords: Motion perception, center-surround interaction, response pooling properties, divisive normalization.

ÖZET

HAREKET YÖNÜ ALGISINDA ÇEVRE BASKILAMASININ KARAKTERİZASYONU

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Görsel algı genellikle, görsel alanımızdaki kişisel bilgileri bir araya getirmemize yardımcı olan çevre modülasyon mekanizmalarıyla elde edilir. Bu mekanizma, hareket algılamasında, hareket yönü algılaması açısından da belirgindir. Merkez-çevre antagonistik bir organizasyon, kolaylaştırma veya baskılama gibi modülasyon mekanizmalarını kullanarak hareket algısına yardımcı olur. Hangi modülasyon türünün rol alacağına dair kararlar genellikle sürüklenen Gabor disk uyarılarının boyutu ve kontrastı değiştirilerek manipüle edilebilir. Bu mekanizmaların sistematik bir araştırması önceki çalışmalarda yapılmadığından, bu uyarıların süre eşikleri arasında kolaylaştırıcı veya baskılayıcı bir örüntü olup olmadığını görmek için üç farklı uyarıcı türü (küçük disk, halka ve büyük disk ızgara uyararı) kullandık. Bunu başarmak adına, insan katılımcıların bu uyarılar için hareket yönü ayırma eşiklerini uyarlamalı merdiven prosedürleri aracılığıyla değerlendirecek davranışsal bir çalışma gerçekleştirdik. Daha sonra, küçük disk-halka-büyük disk ızgaralı uyarı setlerinin süre eşiklerini karşılaştırarak üç olası havuzlama rejimi aradık: verimli veya verimsiz (zayıf veya güçlü baskılama) havuzlama. Büyük disk ızgaraların süre eşiklerinin, her iki kontrast seviyesinde hemen hemen her zaman küçük disk veya halka şeklindeki ızgaralarının süre eşiklerinden daha büyük olduğunu bulduk ve bu da havuzlama rejimlerinden güçlü baskılamayı gösterdi. Ayrıca bölücü normalizasyon modellerinin simülasyonlarını literatürdeki V1 parametreleriyle gerçekleştirdiğimizde modülasyon mekanizmalarının MT parametreleri kullanılarak simüle edilmiş süre eşiklerinde daha belirgin olduğunu gözlemledik. Önceki literatür MT bölgesinin kendi içinde kolaylaştırıcı veya baskılayıcı etkiler ürettiğini öne sürse de, davranışsal verilerimizde gözlemlediğimiz güçlü baskılayıcı havuzlama oluşturan spesifik bir beyin bölgesinin olduğunu öne süremiyoruz. Bu nedenle, bu çalışma gelecekteki nörogörüntüleme çalışmaları için önemli bir sonraki adımdır.

Anahtar sözcükler: Hareket algısı, merkez-çevre ilişkisi, tepki havuzlama özellikleri, bölmeli normalleştirme.



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Chapter 1

Introduction

1.1 Processing Visual Information

Human visual system along with many other species processes light as the primary stimulating source. Light, usually in form of spectral wavelengths, hits our retina and reaches rods and cones. These photoreceptors situated in varying eccentricities process the information coming from the light source along the retina. Cones process mostly foveal or non-eccentric information, detecting wavelength with high acuity caused by lower convergence to ganglion cells, whereas rods process most of the eccentric information, specialized in dynamism of the stimuli. This is the part where phototransduction, in other words the conversion of light energy to electrical energy take place [2].

After energy transduction, rods and cones then project this information to the layer where Bipolar, Horizontal, and Amacrine cells are present. Bipolar cells getting output from rods and cones converge their input via extending their input to retinal ganglion cells. Ganglion cells depending on their receptive field properties, make a summation of these electrical inputs spatially and temporally. Horizontal cells, mostly with inhibitory properties change the overall firing level of these ganglion cells [2].

If a retinal ganglion cell has an ON-center, OFF-surround receptive field, information coming from the central portion of this receptive field has excitatory effects coming from its bipolar cells, which is also known as depolarization. On the other hand, bipolar cells that are located on an OFF-surround portion have inhibitory projections to the relative ganglion cell, which in result hyperpolarize this cell. On the contrary, if the ganglion cell has OFF-center, ON-surround, this layout is wired in reverse, in terms of their excitatory-inhibitory properties [2].

After the summation of total activation, coincidence detectors at the retinal ganglion cell somas compute whether the cell potential pass the threshold. The axons of these retinal ganglion cells then converge their input at the optic nerve. All of the neural connections in this optic tract assembled from one eye then diverge to both hemispheres ipsilaterally and contralaterally. While around 10% of these projections go to superior colliculus and pretectum, 90% of them make connections to lateral geniculate nucleus (LGN), which is located in dorsal part of thalamus [3]. In LGN, types of information coming from rods and cones are relayed, categorized and divided between six different layers consisting of magno- (M-cells), parvo- (P-cells), and konio-cellular (K-cells) cells [4, 5].

These 3 types of cells in LGN have different anatomical structures to better process different aspects of information coming from retina. M-cells located in ventral 2 layers of LGN have more branching, meaning denser and bigger dendritic structures, whereas P-cells located in dorsal 4 layers of LGN have a smaller soma and shorter dendrites. Due to these anatomical structures, M-cells detect small-scale potentials mainly coming from rods in the retina better, which make them more sensitive to temporal frequency (e.g. light detection, motion) and less sensitive to spatial frequency (e.g. edge detection, acuity). On the other hand, P-cells are better processors of color and form by the information coming from the cones in retina, due to their sensitivity to the spatial frequency of a stimulus rather than temporal frequency [6, 7].

All of the processed information in LGN is then sent to primary visual cortex located around the calcarine fissure in occipital lobe. Magnocellular output from LGN is projected onto Layer $4C\alpha$ and parvocellular output to $4C\beta$ [8, 9]. Initial

processing of all visual stimuli takes place here, from edge detection to motion [10]. Neurons in V1, situated in the primary visual cortex or striate cortex, have a topographic center-surround organization and enable humans to detect edges (i.e. spatial frequency) after gathering information on luminance, orientation (simple cells), length (complex cells), and end-stopping (hypercomplex cells) [2]. Namely, low-level properties of the visual field mentioned above are integrated to create a global scene in V1 with the help of these cortical columns. Creation of a scene, by Gestalt principles (i.e. grouping), also affects V1's responsivity to stimuli, because of the feedback connections from upper regions [11].

Having receptive fields in V1, organized topographically to cover entire visual field helps us create a visual scene, when this V1 output from these RFs is sent to upper regions for further investigation of its details. From V1 to V5, also named as medial temporal lobe (MT), other properties of stimuli in our visual field are processed such as color and form (i.e. spatial frequency, including orientation selectivity) starting from V2 to V4 ([12, 13]), motion starting from V3A/B to MT [14, 15, 16, 17]. First pathway starting from V1 to V2 and V4 is called the ventral ("What") stream, which is a pathway to object recognition ending in temporal lobe (e.g. lateral occipital complex, inferior temporal sulcus, fusiform gyrus.) [18, 19]. However, there is another pathway called the dorsal ("Where" or "How") stream, which we will focus on in this thesis. Dorsal pathway starts from V1 and goes through V2d, V3d, V3A/B and then MT, processing the location, orientation, and motion aspects of sensory stimuli. This input from visual cortex ending in MT is then carried to parietal cortex, specifically LIP in posterior-parietal (PP) cortex [20, 21]. These information coming from both pathways are then projected to the sensory and motor regions to carry out goal-directed behavior via categorizing tools and its relative actions [22].

1.2 Motion Perception and MT+ Region

While interacting with outside world, most of the living organisms use motion information to make sense of space around them and how they are positioned in it. In humans and monkeys, area called MT+, which includes MT and MST, processes any motion information coming from the body and striate cortex. This information is then interpreted into motion type, speed, direction to make sense of the scenes using computations as figure-ground segregation [14, 23, 24, 15, 25, 26, 27, 28, 29, 30, 31]. This region therefore processes each aspect of motion from these inputs it receives. As stated earlier, MT is an important region of to process motion perception in dorsal stream. MT takes its marginal input from V3A region, which specifically responds to coherent motion better than V1 and MT, while its neurons better encode absolute disparity [32, 33]. Moreover, human V3A seems to be more selective to "real-motion" compared to homologues in macaques, which is the computed motion after deducing eye movements. Additionally, V3A activity is dependent on the extraretinal components of motion such as anticipation, memory, and attention [34, 17, 35].

With the help of lesion studies, it is also shown that any defect in MT neurons decays motion perception and disparity judgements, without affecting other perceptual processes (e.g. perceiving changes in contrast). In addition to these studies, there are also animal studies which show that microstimulation to MT region creates induced motion perception [36, 37, 38, 39]. MST region, other part of MT+, helps create pursuit eye movements and self motion [40, 41], which are highly tied with creation of optic flow or other types of movements other than translational (e.g. radial, angular) [42, 43]. Researches on dorsal MST (MSTd) (human homologue for MST in macaques) have suggested that this region of the visual cortex is involved in complex calculations that goes into smooth pursuit eye movements and goal-directed behavior [44, 43] and human MST is found to be more responsive to motion than monkeys, although they showed high resemblance in function [45].

After regions MT and MST, dorsal stream continues to areas as LIP and

Broadmann 7a (i.e. posterior superior parietal cortex and intraparietal sulcus), which help with location matching [46], and then connect with ventral stream to carry out processes as integration of sensory and motor functions and goal-directed actions as attending to the saccadic target [47, 48, 49] via predictive remapping of the visual field to stabilize the gaze [50].

In the light of these researches, it is fair to state that human MT+ complex is a region that accumulates necessary motion information coordinated by attention for motor activities and has larger receptive fields in order to scan most of the central visual field while we navigate through world [51, 52, 53].

1.3 Surround Modulation in Visual Perception

As it was stated in the previous sections, visual cortex has topographical mapping in order to better construct outer world. Because visual system is bombarded with information at any given second, to improve accuracy and filtering any unreliable stimuli, these systems should be organized in such a way that it will take information only from a certain portion of visual field for a stimulus and respond only to that portion. Center-surround organization contributes to any kind of visual perception precisely for this purpose. In a classical receptive field (cRF), which propagates a response for a particular type of stimulus (whether it be a certain motion type, its direction, an orientation or color) is modulated by the response of that receptive field's surround portion in an opposite polarization evoked by the same type of stimulus [54, 55, 56, 57].

In motion perception, center-surround interactions are also found to be present. cRFs specialized in processing any aspect of motion is either facilitated (integrative center-surround interactions) or suppressed (antagonistic center-surround interactions), if stimulus is big enough to cover the surrounding regions. Studies done with various animal models suggest that RFs in relevant motion processing regions mostly react to dynamic stimuli (i.e. bars or drifting textures) in an ON-OFF manner [58, 59, 60, 61, 62, 63]. These interactions are also found in humans

in V1 and MT, as well as MST [64, 65, 66].

Although these interactions are shown to be in effect in many organisms, it is also helpful to know that which properties of visual stimuli drive a facilitative or suppressive surround response. Main factors that drive the receptive field surround to propagate a facilitative or suppressive response are stimulus ambiguity and properties as its size and contrast [67, 27, 64, 68] in motion perception. In other words, surround modulation mechanisms in MT neurons increase their facilitative effects to cRFs to decrease ambiguity of stimuli. This may occur in cases where stimulus contrast is low and its size is at a large visual angle [69, 70, 71, 72, 73]. Therefore, facilitation effect increases the reliability of the ambiguous information received by the visual system. On the other hand, in cases where a visual stimulus is in high contrast and relatively medium in size, visual system has enough information to identify stimulus properties (i.e. its shape, motion, location). This suggests that neural image of the stimulus is reliable and not ambiguous. However, because stimulus has an increased size and contrast, activation as response to this stimulus is quite large. Therefore, surround modulation mechanisms suppress the activation in cRF, as studies with macaque monkeys show [74, 75, 76]. In later stages, different motion information may be used to infer form, which may be used for figure-ground segregation [77, 78, 79, 80, 81].

1.4 Computational Models in Motion Perception

All cognitive processes within the brain are executed via input to an organism in the form of sensation. These inputs then are translated to electrical responses in different types of neurons in different layers and locations in the cortex. However, main concern on how these individual neurons interact with one another to create high-level cognitions is still studied to this day. Studies investigating neural networks usually are used via identifying a population of neurons (population usually indicates an arbitrary number of neurons). Because connectivity between

neurons and their input-output systems resembles an electrical circuit, it was possible to imitate neuronal response under certain circumstances, knowing how they operate together [82, 83, 84, 85, 86, 87, 88].

These computational models also allow us to predict neuronal responses made in visual perception. For instance, divisive normalization model [87] was first used for computing the amount of activation within an arbitrary field of striate cortex upon viewing grating stimuli. This arbitrary field may consist of a foveal or peripheral region of the striate cortex, containing an arbitrary number of neurons. Because any neuronal population within striate cortex has center-surround antagonistic properties, computations for those regions were made accordingly. This model specifically suggests that any activation caused by viewing a stimulus would be divided by suppressive activation caused by the same stimulus. This division then allowed us to make three conclusions, which were in line how neurons in sensory regions work [89]. First of them was response saturation. As a certain level of stimulation is passed (e.g. high-levels of contrast, brightness etc.), overall neuronal response saturates to a sustained level of activation, due to this division. Second one regards preferred stimuli between neurons. A single neuron or a neuronal population will always respond more to preferred stimulus rather than non-preferred one. This is caused by the stimulus drive computed in numerator portion in the divisive normalization models. Lastly, when we view multiple stimuli, their response will be calculated after giving each of them weights as an indicator of importance. This weight is then multiplied by the stimulus drive, causing it to have a higher response (or having the spotlight, e.g. $\beta = 1$) or causing it to be simply ignored (e.g. $\beta = 0$). These weights may also be called attentional drive.

This model may be applied to both sensory perception procedures and higher-level cognitive functions due to its great flexibility in modulating presented stimuli, its location, its importance, and the amount of facilitative/suppressive drives via changing designated parameters. Consequently, to compute neuronal response to visual perception processes, computational models simulate populational response regarding the center-surround antagonistic mechanisms within that population. As coincidence detectors sum activation temporally and spatially to fire

a neuron, a cognition or a perception is also achieved by this framework [90, 91]. Therefore, by normalizing these individual neuronal responses over an arbitrary population that has surround modulation mechanisms, we achieve sensitivities to different stimuli properties such as orientation, spatiotemporal frequencies, and contrast.

As stated earlier, literature has shown that motion perception, based in MT, works with surround modulation. These studies employ behavioral and brain imaging techniques to unravel modulation mechanism using disc gratings. Studies predicting neural responses to visual stimuli have been tested on both receptive field properties of V1 and MT [92, 93]. These studies were using grating stimuli that are different in size and contrast using discrimination thresholds and BOLD responses as their measuring unit to compute facilitative and suppressive activation caused by viewing these stimuli [71, 72, 73]. However, because receptive field properties change as we move from V1 and MT, properties of neuronal responses will change undoubtedly. On the grounds that MT neurons respond to global motion more than V1 and V1 is only selective to two-dimensional motion [15, 94, 95], we may assume that MT models of divisive normalization methods would produce more similar results to normalized response given to those stimuli, compared to results of V1 model in terms of duration thresholds [93]. In other words, because MT allows us to have a final verdict on motions and its properties, MT models would be ecologically more valid. Since normalized responses in these studies are derived from the predicted duration thresholds of motion discrimination, we may also deduce that behavioral duration threshold data gathered from a set of stimuli will be more consistent with simulated thresholds using MT parameters from literature.

One may compute responses made to visual stimuli utilizing divisive normalization models in two different ways. However, these ways correspond to different types of response calculation. First of them is the winner-take-all approach [89]. This approach allows us to compute the highest response produced by a single-unit neuron from a pool of neurons (arbitrary population of neurons). This also suggest that the neuron that conducts the highest response for a particular stimulus is the most sensitive to that stimulus. Meaning that, this approach enables

us to predict sensitivity, therefore sensitivity of any stimulus change via max-pooling, which is selecting the highest responding neuron. Second one usually relates to brain imaging methods more due to differences on response computation method and called populational summation approach. In this approach, we sum responses from the neurons that are more responsive to a stimulus. Hence, all responsive neuron outputs (as in cRFs) are pooled together as one. On the other hand, these two different approaches may also differ in terms of predicted response patterns in V1 and MT. This may due to previous research stating that V1 generally acting as a suppressive region to all visual stimuli [96], whereas MT is more indicative of motion stimuli [15, 94]. Winner take all approach computes neuronal response being mostly suppressive, which produces a decline in normalized responses as stimuli gets bigger in size, regardless of its contrast [93] in V1 models. Still, its results using the parameters for MT and hMT+ models are consistent with behavioral data. [92, 93]. On the other hand, it is suggested that responses predicted with population summation approach are consistent with normalized responses gathered from brain imaging results than winner take all approach.

In addition to models suggested above, other neural network models suggest that amount of the MT activity and perception may not always match and is actually dependent on stimulus contrast. Motion contrast and motion integration [97], is two distinct responses given to moving grating stimuli, indicating that there is an illusory motion of aperture in the opposite direction or the same with the grating, respectively. These two illusory motion are thought to be driven by the segmentative and integrative modulatory effects of the surround, which are representative of inhibitory or excitatory effects. In this sense, if the cRF contrast of the stimulus is low and therefore yields ambiguous information, surround should integrate its activity to cRF, to form a uniform perception and motion integration, whereas in the case that information is not ambiguous, surround should be segmentative, creating a motion contrast. However a study done by Huang and his colleagues revealed that this contrast dependency in perception and neuronal activation may be conflicted [68]. This study has shown that processing ambiguous stimuli in cRF may elicit surround integration behaviorally but MT

activity would yield segmentation. Another issue in computational models of motion is the aperture problem. Since the motion perception is temporally dynamic and changing [98, 99], once V1 is activated, processed information may not be accurate due to ambiguities in end-stop cells in V1. Therefore, verdict on motion direction is delayed until responses are transformed from orientation-dependent to motion-dependent. Therefore neural networks were developed to solve these problems via implementing a divisive normalization model for surround input. Specific to this computational model another set of suppressive input at the extent of cRF is also added to the model to simulate V1 end-stop cell outputs [100]. Therefore, while there are many aspects to be taken into account in motion perception, using divisive normalization models seems to be a promising tool to predict behavioral responses to drifting grating stimuli.

1.5 Research Gap and Possible Pooling Regimes

Motion perception studies suggested that differences in low-level features of visual stimuli (i.e. size and contrast) such as drifting Gabor gratings have an effect on discrimination duration thresholds [92, 71, 73, 93]. These changes in discrimination thresholds are a result of surround modulation mechanisms inside our visual system. There are two of these modulation mechanisms, which are facilitation and suppression. Moreover, facilitation and suppression make computational properties of our visual system nonlinear.

To measure effects of this mechanism, visual drifting stimuli is widely used. By changing the size and the contrast of these stimuli, we see a repeated pattern of results throughout the literature: With large stimuli, as the contrast increases, it is harder to detect motion direction. On the contrary, increasing the size facilitates the motion perception if the stimulus has low contrast. However, human studies conducted on this topic were mainly done with disc gratings varying in size and contrast. Yet, only in animal studies [70] annular gratings with disc gratings were measured in terms of single-cell electrophysiological responses. The importance of studying annular grating emerges from the very idea of receptive

fields. Receptive fields consist of two portions: a classical receptive field (cRF, also known as center) and receptive field surround. Therefore, studying with disc gratings behaviorally gives us insight to responses only made to cRF and the entirety of RFs depending on the stimulus size (small and large stimuli, respectively), but not to sRFs. Duration thresholds to annular gratings may give us an insight to responses produced by sRFs. Owing to the lack of research done with annular gratings in humans and how cRF and sRF interacts with each other to complete the receptive field poses as a gap in the literature. Seeing whether the sum of small disc and annular gratings is greater than large disc stimuli in our behavioral results and seeing whether behavioral data is consistent with model results using parameters for both V1 and MT regions then becomes our main research interest for this study.

To do this, we first looked into the stimulus size and contrast levels, that are mostly used in the previous literature [92, 71, 73, 93]. While doing this, we have also looked for particular size and contrast levels that best produce facilitation and suppression effects regardless of them being behavioral or brain imaging studies. As a result, we have picked 1° , 2° , 5° , and 12° (diameter) as our grating size levels. On the grounds that 1° and 2° is considered as small gratings and 5° and 12° gratings as large ones, we have also decided to take these size levels as our small and large gratings, respectively. For our annular gratings, we have assigned our small grating sizes as inner diameter size of our annular gratings. Moreover, we also assigned our large grating sizes as our outer diameter size for annular stimuli.

Being able to see whether "the sum is greater than its parts", we try to look for any response pooling properties between small disc, annular and large disc drifting gratings as they may reflect RF portions and RFs or higher-level decision areas. These pooling properties may in the end be efficient or inefficient. As you may see in Figure 1.1, let us suppose that in V1, n_1 consists of a neuron population within a cRF, and n_2 is in sRF. n_1 and n_2 generate their own outputs according to the input they are receiving on visual stimulus. This stimulus can be a small grating for n_1 and an annular grating for n_2 . From their neuronal population level, they will extend their outputs to a higher-level decision area in

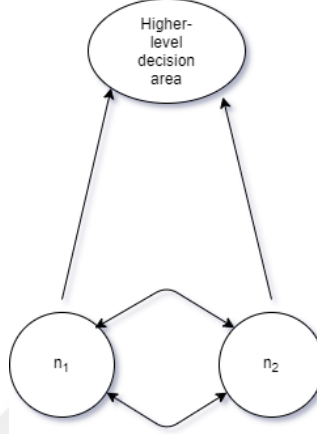


Figure 1.1: A flowchart of the connections within an RF and between RF and higher-level decision areas. n_1 and n_2 are neuron populations in center and surround portions of an RF, making cRF and sRF. Higher-level decision area is any neuron population from dorsal ("Where", "How") stream, which could be anywhere from extrastriate cortex to MT, or other areas as LIP, Brodmann 7a, etc. [1]

MT, which may decide what to do about this information. Output extended to this area will in this case be motion direction information, and decision area will ultimately decide on overall motion properties along with direction and help to create goal-directed behavior, for instance. Therefore our main goal in this study is to look at whether this pooling from small disc and annular gratings to large disc gratings are efficient in terms of behavioral duration thresholds of human participants; and to see whether divisive normalization model predictions using both V1 and MT region parameters agree more with behavioral results.

We have deduced our predictions on pooling properties based on our flowchart on neuronal populations, shown in Figure 1.1. Firstly, we will demonstrate the our first possibility, efficient pooling. This possibility indicates that populations n_1 and n_2 process the visual information such as small disc gratings and annular gratings, respectively. While this processing happen, a winner-take-all approach might be taken to predict response to these stimuli. This means that the highest response of that neuron population, in other words, the response produced from the most sensitive neuron to that stimulus will directly be sent to higher-level area. Then, this area will decide on its output based on this single output of

that neuron. On the other hand, while higher-level area makes a decision after n_1 and n_2 send their outputs, final outcome may be delayed due to inefficient pooling. Meaning that, once n_1 and n_2 send their outputs to this area, one of them will be suppressed by the higher-level decision area to reach a conclusion on the visual information. Therefore, this suppression by higher-level area will cause an increase in duration thresholds or decrease in overall neuronal response, causing the inefficient pooling. This is the weak suppression possibility. Lastly, because of the RF properties within neuronal populations representing cRF and sRF, the outputs from n_1 and n_2 may be suppressed even between themselves before they are sent to higher-level area. Meaning that, the suppression coming from both within and between higher- and lower-level neuronal populations may produce a stronger suppression; and this would be strong suppression possibility.

To look for any type of pooling between different RF portions and the whole RF, we decided to conduct a behavioral study first and simulate duration thresholds for these stimuli accordingly using divisive normalization models. Namely, we investigated these center and surround interactions in terms of pooling properties between small disc, annular, and large gratings representing cRF-sRF-RF utilizing duration thresholds in both experiments. To investigate these effects for cRF, we will use duration thresholds of small discs; for sRFs, we will use annular stimuli; and for whole RF (cRF and sRF), large discs will be utilized in both behavioral study and normalization models.

For our behavioral results, we expect our duration threshold results regarding the disc gratings be similar to the previous literature. Meaning that, we expect increasing discrimination thresholds in high contrast as the stimulus size increases and we expect a decrease in thresholds in low contrast as stimulus gets bigger. On the other hand, although research examining annular and discs gratings together is studied in animals via spike responses [101, 102], there are no studies done with only annular gratings to our knowledge. Therefore, we will explore different possible pooling outcomes between duration thresholds of our stimuli, presenting them individually. We also hypothesize that divisive normalization model will successfully explain the empirical results, according to recent studies [93, 92].

For the pooling outcomes, there are three different possible regimes that we may observe in behavioral data: Efficient pooling, weak suppression, and strong suppression. Let us assume, sensitivities are driven from motion discrimination thresholds calculated for different grating stimuli. While looking at different possible regimes, we may utilize these thresholds as T (for center, small disc, cRF: T_s , for surround, annular, sRF: T_a , for whole RF, large disc: T) for our behavioral study and normalization model and define S as behavioral sensitivity or overall response for these stimuli:

$$T \sim 1/S, \quad (1.1)$$

$$S \sim R(x, \theta, c)/\textit{Criterion}, \quad (1.2)$$

$$T \sim \textit{Criterion}/R(x, \theta, c), \quad (1.3)$$

where T is duration threshold produced by an arbitrary neuronal population at position and orientation space (x, θ) to a stimulus scaled by contrast level c , and *Criterion* is a constant for saturation contrast. To calculate our first possible regime efficient pooling, we assumed that:

$$T \leq \min(T_s, T_a), \quad (1.4)$$

where T , duration threshold produced by neuronal population to large grating, would be less or equal than duration thresholds to small disc grating (cRF, T_s) and annular grating (sRF, T_a).

For weak suppression possibility, we may assume that duration thresholds to large disc stimuli (T) will be in between threshold levels of small disc (T_s) and annular grating stimuli (T_a):

$$\min(T_s, T_a) < T < \max(T_s, T_a). \quad (1.5)$$

Finally, for our strong suppression regime, we expect thresholds measured for large disc stimuli (T) will be higher than threshold levels of both small disc (T_s) and annular grating stimuli (T_a):

$$T > \max(T_s, T_a). \quad (1.6)$$

After checking for these relationships in our behavioral data, we will also check for these in duration thresholds computed by divisive normalization models, using parameters from literature for V1 and MT to see if they are consistent with our behavioral data.



Chapter 2

Methods

2.1 Behavioral Experiment

2.1.1 Participants

8 participants participated in this experiment (3 male, 5 female from an age range of 22-30). Participants had normal or corrected-to-normal vision as they reported before the experiment. No participant has claimed to have a neurological or visual disorder. All participants were given informed consent in a written form to participate in our study, which is approved by the Research Ethics Committee of Bilkent University. They were briefed about the experimental procedure prior to the first session.

2.1.2 Stimuli, Experimental Procedure, and Analyses

Experiment was carried out in National Magnetic Resonance Research Center (UMRAM) in Bilkent University. A CRT monitor (HP P1230, 22 inch, 1280x1024 resolution, 120 Hz) was used to present our stimuli. Participants were seated in a chair, 75 cm away from this monitor. They rested their heads on a chin-rest to

view the stimuli without any head tilting or any other head motion. The chin-rest also allowed us to align participants' gaze to be centered to the monitor. All responses were collected via key press from a standard USB computer keyboard. A look-up table was prepared via screen characterization (SpectroCAL, Cambridge Research Systems Ltd., UK) on gray-scale for measuring and making sure luminance values used for our behavioral setup does not change across trials.

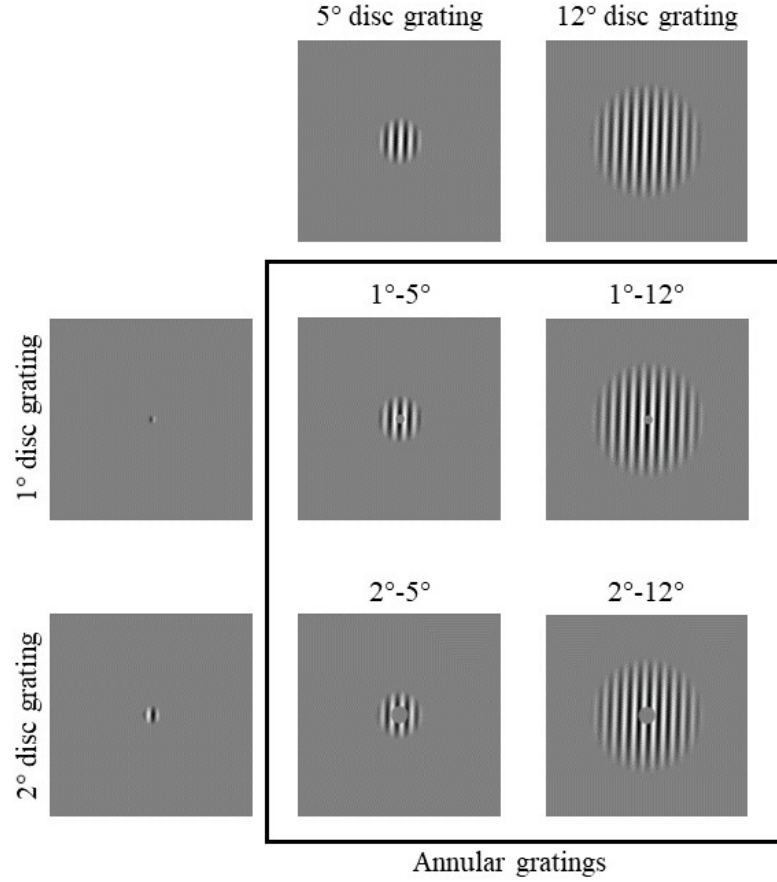


Figure 2.1: All gratings used in the behavioral experiment.

Our stimuli were drifting vertical sine-wave gratings (Spatial Frequency, SF: 1 cycle per degree, Speed: 2 degrees per second) with a raised cosine filter to blur the grating edges by the radius of each stimulus. The reason that we did not use a two-dimensional isotropic Gaussian envelope was due to the usage of annular stimuli. Application of Gaussian blur to both inner and outer circles of annuli made stimulus contrast drop significantly. We had eight stimuli in total,

after selecting two sizes for small and large discs. Consequently, we had two small grating discs (1° and 2°), two large grating discs (5° and 12°), and four annular stimuli (outer edge: 5° -inner edge 1° , 5° - 2° , 12° - 1° , 12° - 2°) (Figure 2.1). We have used MATLAB version 2018b with Psychophysics Toolbox Version 3 (PTB-3) [103] to generate our stimuli.

There were two sessions for the behavioral part of the experiment, varying in contrast (Low contrast condition: %10, High contrast condition: %98). Behavioral data to stimuli differing in contrast were collected in separate sessions, in case of a possible adaption to the high contrast level. Each of these conditions were then presented around a fixation point at the center of the monitor on a mid-gray background (16.86 cd/m^2). Each stimulus appeared central to the monitor with a random drifting direction.

To detect motion discrimination thresholds for each condition, we implemented two interleaved 3-up-1-down adaptive staircase procedures starting from different durations (50-150 ms). A Gaussian temporal ramp was used for changing contrast in the experiment. Ramps were fitted to the duration of the stimulus calculated by the staircase. Finally, there were 120 trials for each staircase totaling 240 trials for each stimulus. For each experiment session, participants were instructed to fixate on a point at center of the screen. After 500 ms, a stimuli drifting left or right appeared centered on the fixation point for the duration calculated by the staircase. After stimulus offset, participants reported stimulus' direction via a two alternative forced choice answer, pressing left or right arrow keys on USB keyboard of the computer. After 500 ms, next stimulus appeared (Figure 2.2)

To fit psychometric functions to our data (logistic function) and estimate discrimination thresholds for each participant and stimuli, we used Palamedes toolbox [104] using a 79% accuracy rate. We have also used the same tool to measure duration threshold SEMs via bootstrapping, which may both be found in Appendix. For all participants and conditions, we agreed a priori upon that no goodness-of-fit value below 5% of any stimulus duration threshold will be taken into final analysis while fitting logistic functions [105].

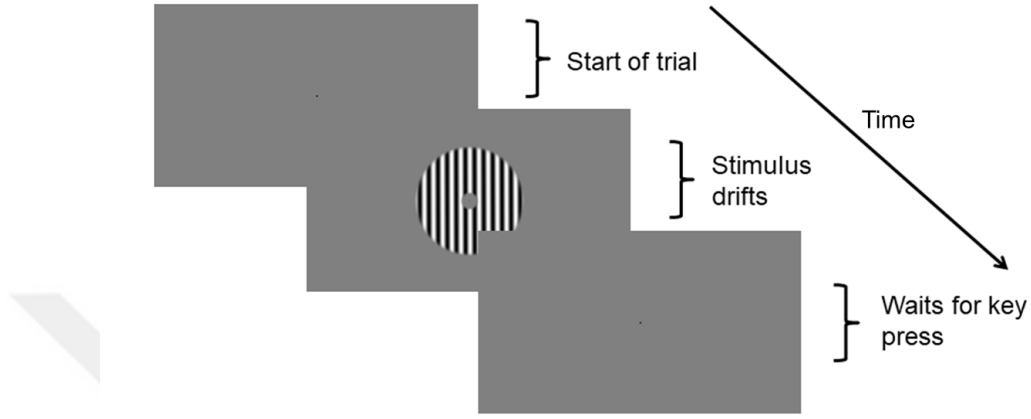


Figure 2.2: Behavioral experiment procedure.

Once we gathered all duration thresholds for each small disc-annular-large disc grating triples from each participant, we looked at possible pooling properties between them according to Eq. 1.4, 1.5, and 1.6. According to duration threshold of large disc grating being lower, in between, or greater than the small disc and annular grating thresholds, we identified possible efficient and inefficient pooling regimes. As in Figure 1.1, let us say that n_1 is the neuronal population that is activated by small disc grating and n_2 is activated by annular grating and may be representative neuronal populations of center and surround parts of a single receptive field respectively. The sensitivities evoked by the small disc and annular gratings (Eq. 1.2) would then be combined if we present a large disc grating, since it is the visual summation of small disc and annular ones. In this sense, there are these three possibilities for pooling information of both n_1 and n_2 while viewing large disc gratings. This combination of information can be effective, meaning that there would be no suppression between the neuronal populations that process these stimuli. On the other hand, information may be pooled ineffectively, meaning that some information while processing gets lost due to the inhibition taking place at those two neuronal populations. Hence, as suppression gets stronger when processing a large disc grating, sensitivity evoked by that grating will be lower. We may then derive duration thresholds from possible sensitivities, which could be higher or lower due to suppression strength

with Eq. 1.1. In conclusion, comparing duration thresholds of these three grating stimuli could reveal information about characterizations of surround suppression by these pooling possibilities.

To follow-up, we decided to carry out a two-way repeated measures ANOVA between stimulus levels varying in size and stimulus type (small, large disc or annular grating) and contrast to see whether our results are able to replicate previous studies. Paired-samples t-tests were used for looking further into pairwise comparisons. To avoid a Type I error, Bonferroni corrected α was determined to be $p = 0.003$.

2.2 Divisive Normalization Model

For this study, we have used divisive normalization model to simulate population neuronal responses to circular Gabor grating stimuli [87, 88]. We have implemented a version of this model similar to [92, 93], which is shown to account for surround modulation via describing a stimuli at (x, θ) in contrast level c :

$$R(x, \theta, c) = \frac{E(x, \theta, c)}{S(x, \theta, c) + \sigma}, \quad (2.1)$$

where E and S are excitatory and suppressive drives and σ is a positive constant called semi-saturation contrast. Excitatory drive is the neuronal response given in an arbitrary neuronal population to a stimulus positioned in (x, θ) , scaled by contrast c :

$$E(x, \theta, c) = e(x_e, \theta_e, c) * N(x, \theta, c), \quad (2.2)$$

where e is the excitatory kernel applied to a space (x_e, θ_e) with contrast level c . This excitatory kernel is then convolved with a neuronal image (N) of a stimulus applied with a Gaussian filter, which have two dimensions (x, θ) and scaled by the same c . After computing our excitatory drive, we then convolve it s to find our suppression drive, S :

$$S(x, \theta, c) = s(x_s, \theta_s, c) * E(x, \theta, c), \quad (2.3)$$

where s is our suppression kernel positioned in (x_s, θ_s) and scaled by contrast level c . Therefore, applying our suppression kernel s to our excitatory drive N 2.3, gives us responses of each neuron across our summation field to stimulus in the spatial extent (x, θ) in c contrast level. To find the populational responses, we summed all R values at ± 5 to the stimulus center (x) , scaled by c , according to the population summation approach [93]:

$$R(c) = \sum_{x \in P(s)} \sum_{\theta} R(x, \theta, c). \quad (2.4)$$

To implement a single-unit response approach, which employs winner-take-all solution [92], we found the maximum value that R takes, as indicated below:

$$R(c) = \max(R(x, \theta, c)). \quad (2.5)$$

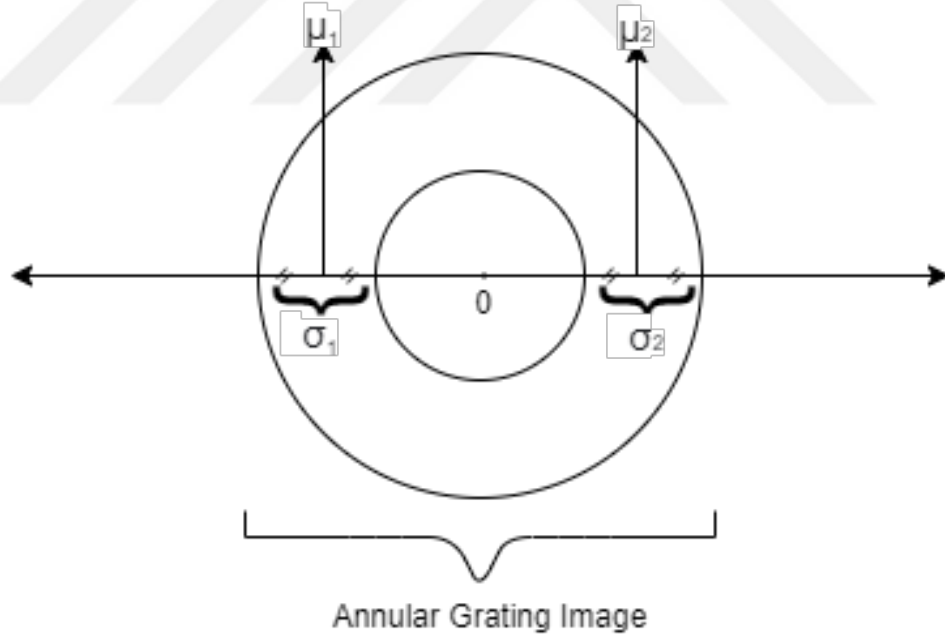


Figure 2.3: Parameters (μ and σ) of our neural image, while creating an annular grating.

Addition to the small and large Gabor disc gratings, which allows us to reflect a light to surround modulation mechanisms in cRF and the whole RF, we also needed to implement this model to annular gratings. To do this, in Eq. 2.2, we have changed our neural image N to be an annular grating. In order to create disc gratings, $N(x, \theta, c)$ is computed via applying a Gaussian filter to a stimulus

in (x, θ) scaled by contrast c . Therefore, while applying this filter, its spatial extent becomes x . Then, our mean, will be the eccentricity from center, which is denoted by μ ($\circ$). Finally, our σ will be the size of our stimulus in diameter. A diagram of these parameters may be found in Figure 2.3. After we summed these two different N s, they are then convolved by our excitatory kernel as in Eq. 2.2. These two N s were the neural images centered to the midpoints of our annular gratings centered on 0, which took the width of annular grating as its size. Then our parameters for annular grating neural image became:

$$\mu_1 = -|size_s - size_l|, \quad (2.6)$$

$$\mu_2 = |size_s - size_l|, \quad (2.7)$$

$$\sigma = |size_s - size_l|, \quad (2.8)$$

where $size_s$ is the size of small grating and $size_l$ is large grating size in degrees; μ_1 and μ_2 are the mean values for our annular gratings midpoints and σ is the width of the annular grating. After defining our parameters, we took x for our application space for our Gaussian filter as we did for creating neural images for disc gratings. Finally, we have summed two neural images created in (x, θ) dimensions were convolved with the excitatory kernel to result in our excitatory drive for annular gratings (Eq. 2.2). You may find the code file to create these images in the Appendix.

This model was implemented from the models developed by Er and his colleagues (2020) and Schallmo and his colleagues (2018), utilizing MATLAB R2018b to create our simulations (see Table 2.1 for model parameters). Excitation and suppression summation and orientation kernel widths are adjusted to fit behavioral data in literature.

Table 2.1: Model parameters from previous literature for areas V1 and MT.

Symbol	Description	Value	
		V1	MT
c	Stimulus contrast	0.1, 0.98	0.1, 0.98
x_e	Excitatory spatial summation kernel width	2	5
x_s	Suppressive spatial summation kernel width	5	20
θ_e	Excitatory orientation summation kernel width	8	20
θ_s	Suppressive orientation summation kernel width	10	50
σ	Semi-saturation constant	.0002	.0002
$P(s)$	Neighborhood of stimulus position (in x dimension) in “Population Responses”	± 5	± 5

Chapter 3

Results

3.1 Behavioral Experiment

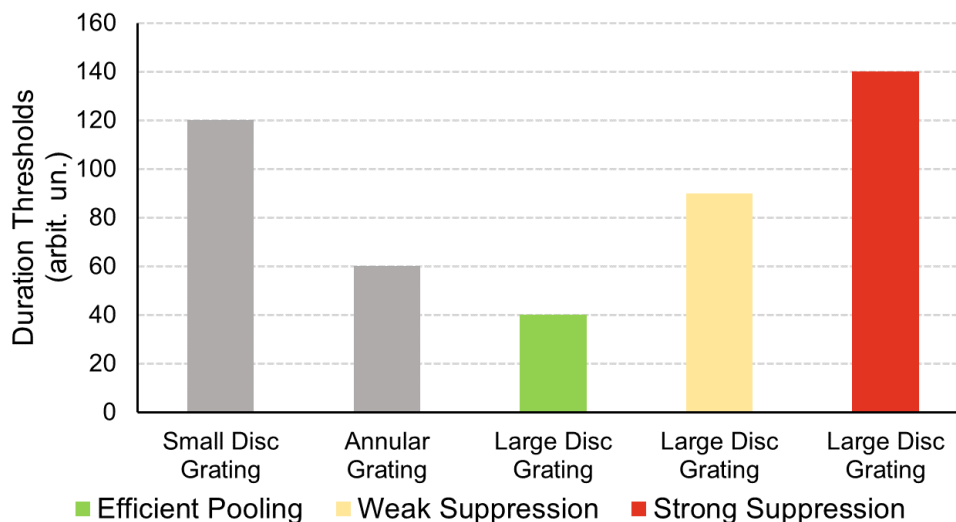


Figure 3.1: Possibilities for how thresholds levels will change for different types of stimuli in both behavioral data.

We aimed to investigate how visual information while viewing matching drifting grating stimuli utilizing behavioral duration thresholds and then see whether simulated duration thresholds for these stimuli in divisive normalization models

are consistent with our behavioral data. As you may see in Figure 3.1, these three possibilities are:

- *P1*. Efficient pooling: Thresholds computed for drifting large disc gratings will be lower than or equal to the ones for small disc and annular gratings.
- *P2*. Inefficient pooling I: Weak suppression. Thresholds computed for drifting large disc gratings will be greater than the minimum value of the thresholds computed for small disc and annular gratings, and it will be lower than the maximum value of the ones for small disc and annular gratings.
- *P3*. Inefficient pooling II: Strong suppression. Thresholds computed for drifting large disc gratings will be greater than the ones for small disc and annular gratings.

Table 3.1: Possible pooling properties examined for the duration thresholds from behavioral data: Efficient (efficient pooling), Weak S. (weak suppression), Strong S. (strong suppression).

Contrast	Stimulus Size Couples	Pooling
Low	1°-5°	Weak S.
	2°-5°	Strong S.
	1°-12°	Strong S.
	2°-12°	Strong S.
High	1°-5°	Strong S.
	2°-5°	Strong S.
	1°-12°	Strong S.
	2°-12°	Strong S.

According to these three possibilities combination or pooling of information coming from both small disc and annular gratings will be either efficient or inefficient. In Table 3.1, you may see that comparing duration thresholds of our stimuli revealed that information from small disc and annular grating is pooled inefficiently. As you may see from our behavioral results, changes in duration thresholds of each stimuli show strong suppression, which indicates that duration thresholds of large disc gratings are higher than small disc and annular gratings.

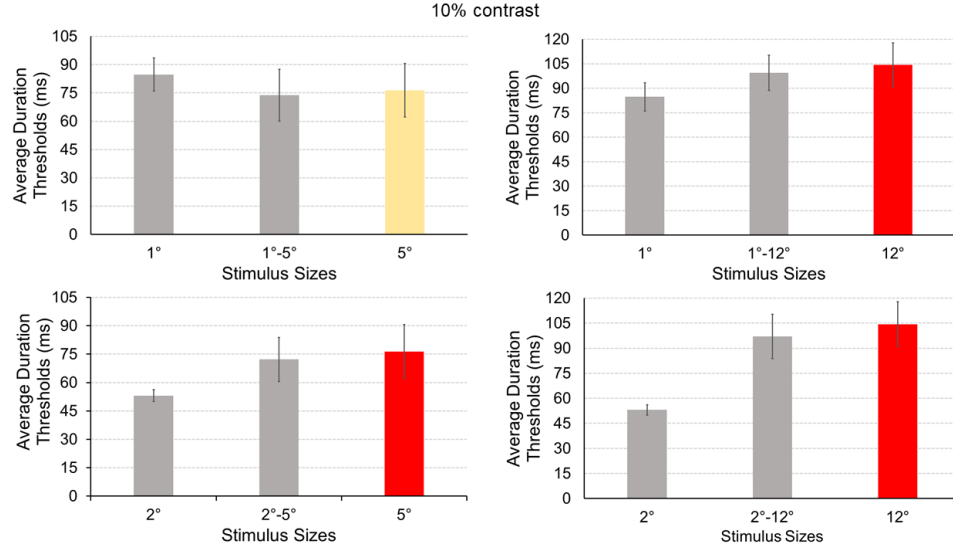


Figure 3.2: Possible pooling properties between small disc-annular-large disc triples examined using averaged motion discrimination threshold (milliseconds) changes in low contrast (10%). Efficient pooling (green), weak suppression (yellow), strong suppression (red).

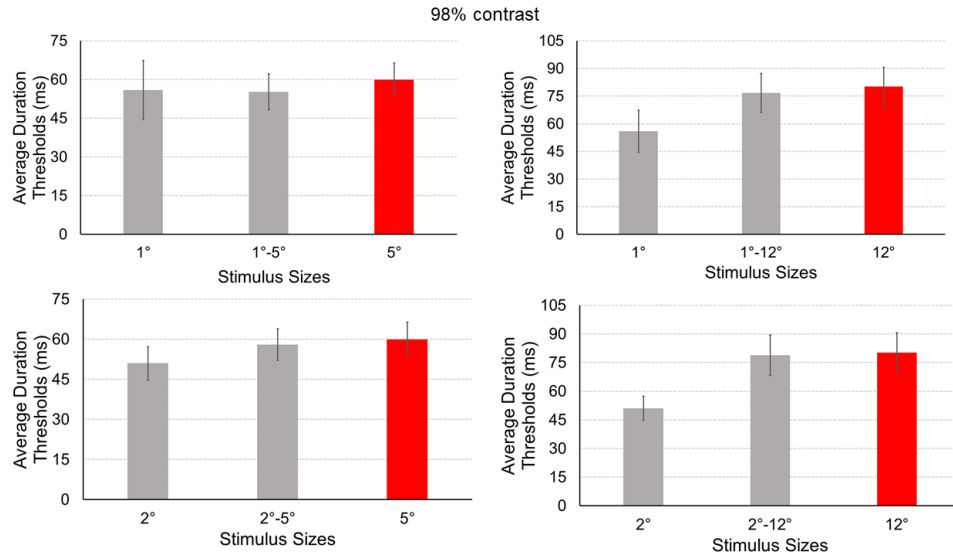


Figure 3.3: Possible pooling properties between small disc-annular-large disc triples examined using averaged motion discrimination threshold (milliseconds) changes in high contrast (98%). Efficient pooling (green), weak suppression (yellow), strong suppression (red).

Therefore, $P3$ is consistent with behavioral data. Figures 3.2 and 3.3 show which pooling property is existent in different stimuli triples (small-annular-large) more clearly. You may see large disc grating averaged motion discrimination thresholds from our behavioral experiment are almost every time greater than the other two, which was our strong suppression possibility.

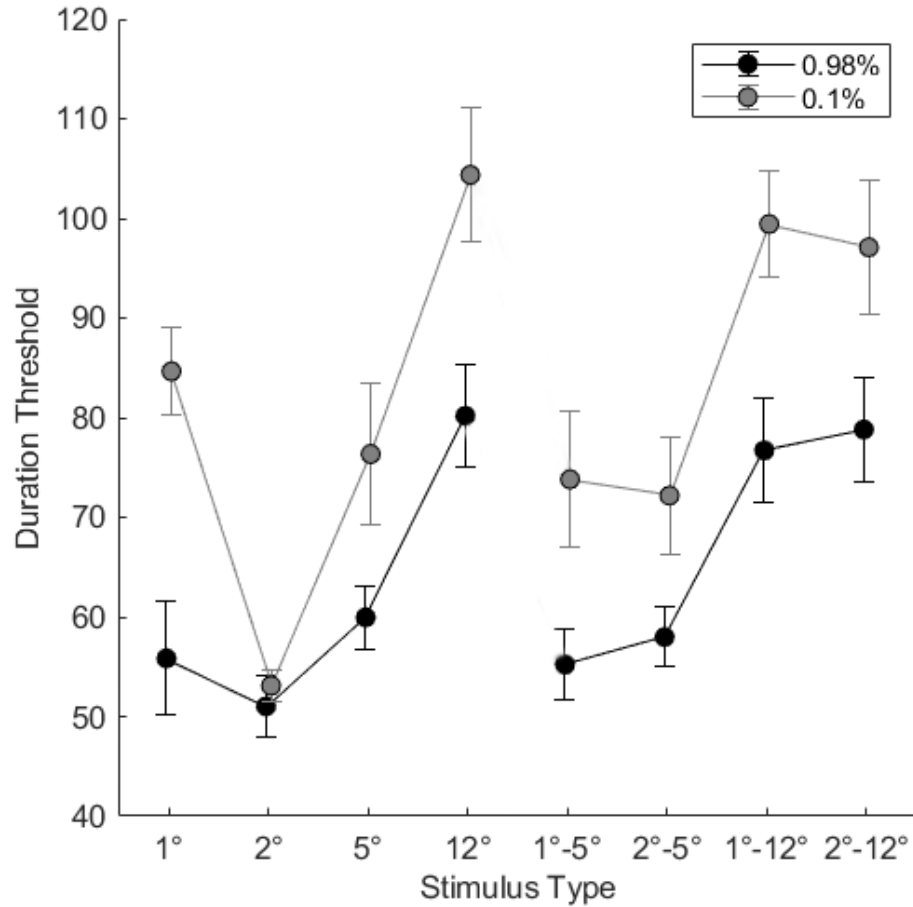


Figure 3.4: Average motion discrimination threshold (milliseconds) changes between different stimulus sizes (in degrees) and contrasts (percent level). First four in disc gratings (1°, 2°, 5°, 12°), last four annular gratings (1°-5°, 2°-5°, 1°-12°, 2°-12°).

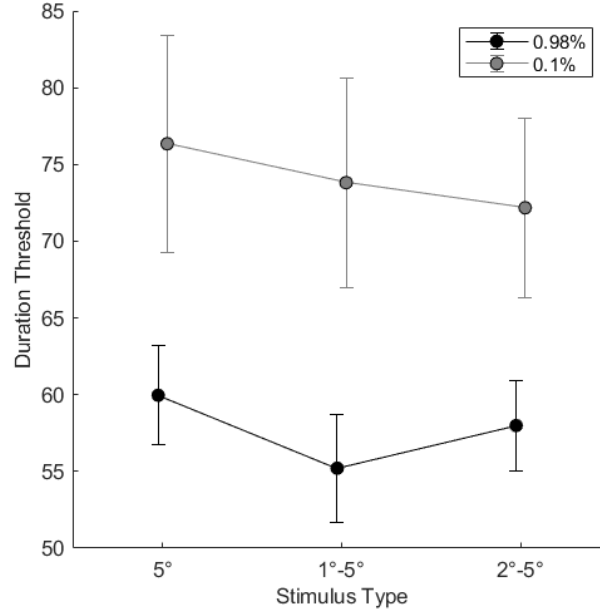


Figure 3.5: Average motion discrimination threshold (milliseconds) changes between 5°, 1°-5°, and 2°-5° and contrasts (percent level).

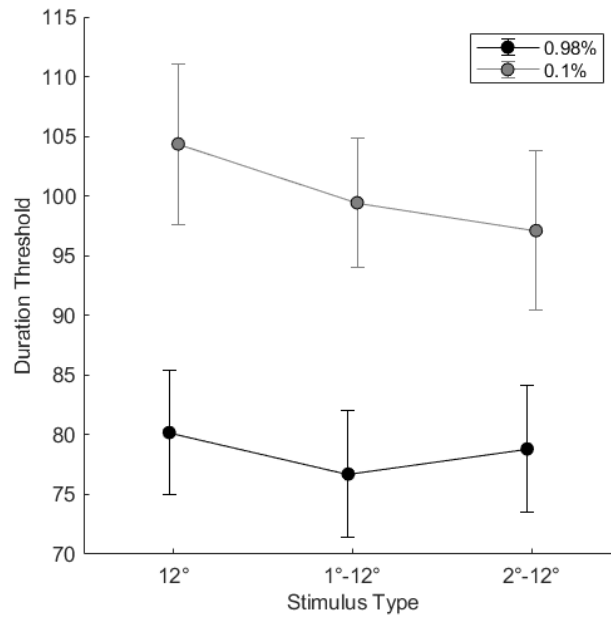


Figure 3.6: Average motion discrimination threshold (milliseconds) changes between 12°, 1°-12°, and 2°-12° and contrasts (percent level).

3.1.1 Inferential Statistics Analyses

Our experimental design successfully replicated the previous literature for disc gratings: As size increased in high contrast, motion discrimination thresholds have increased. Whereas in low contrast, there was a duration threshold drop due to facilitative effects of surround. Therefore, we observed a systematic change in duration thresholds as size and contrast differs in disc gratings (Figure 3.4).

A two-way repeated measures ANOVA showed a significant interaction effect between different sized stimuli and contrast ($F(7,49) = 5.14, p < 0.0001$) (Figure 3.4) with a large effect size ($\eta^2 = 0.423$). Additionally, there were significant main effects of contrast ($F(1,7) = 68.22, p < 0.0001$) with a large effect size ($\eta^2 = 0.907$) and stimulus type ($F(7,49) = 22.34, p < 0.0001$) also with a large effect size ($\eta^2 = 0.761$). In terms of simple effects, our stimuli also differed in duration threshold due to contrast change in 1° ($F(1,7) = 21.46, p = 0.002$), 5° ($F(1,7) = 6.95, p = 0.03$), 12° ($F(1,7) = 15.12, p = 0.005$), 1° - 5° ($F(1,7) = 8.95, p = 0.02$), 2° - 5° ($F(1,7) = 5.21, p = 0.05$), 1° - 12° ($F(1,7) = 13.36, p = 0.008$) and 2° - 12° ($F(1,7) = 8.65, p = 0.02$). The only stimulus that did not differ in duration thresholds by contrast change was 2° disc grating ($F(1,7) = 0.11, p = 0.7$), caused by a sudden drop of threshold in low contrast, which made thresholds from both contrast levels almost identical. Finally, all duration thresholds for different stimuli differed within both in low ($F(7,49) = 7.89, p < 0.0001$) and high ($F(7,49) = 16.21, p < 0.0001$) contrast. This suggests that there is a meaningful difference as we change sizes of our stimuli.

After finding these significant effects, we also wanted to look at differences in duration thresholds between small disc-annular-large disc triples in which annular grating inner circle diameters change. However, we could not find such systematic change. Annular gratings differing in inner diameter size (1° or 2°) and its disc grating counterpart (5° or 12° discs) did not have any meaningful differences in terms of duration thresholds (Figures 3.5 and 3.6).

To see if there are any differences between small disc-annular-large disc triples, we have conducted pairwise comparisons via using paired-samples t-tests.

These tests only shown that duration thresholds for 12° ($p=0.009$, $M=104.36$, $SD=19.13$) was significantly higher than 2° - 12° ($M=97.10$, $SD=18.87$) in low contrast.

For our annular stimuli, we conducted a two-way repeated measures ANOVA as an additional comparison (Figure 3.5 and 3.6). There were no difference between 5° , 1° - 5° , and 2° - 5° across contrast levels ($F(2,14) = 0.57$, $p = 0.576$). This was the same with 12° stimuli ($F(2,14) = 2.88$, $p = 0.090$). However, 5° disc and annular gratings differed not in between themselves ($F(2,14) = 2.42$, $p = 0.125$) but with contrast ($F(1,7) = 19.65$, $p = 0.003$), as 12° disc and annular gratings also did not differ between themselves ($F(2,14) = 2.99$, $p = 0.083$) but with contrast ($F(1,7) = 42.97$, $p = 0.0003$).

Overall, we found that size and contrast together have systematically changed behavioral duration thresholds for our contrast and size level, as the previous literature has shown. Our analyses have also shown that size and contrast separately also changed duration thresholds. Only in 2° gratings, there was no effect of contrast due to a drop in duration thresholds caused by facilitation. At both contrast levels, duration thresholds were increased as the stimulus size increased, which also may be considered as a suppression effect. Annular grating inner circle sizes did not have any effect on duration thresholds in both 5° and 12° annular gratings. Therefore whether the inner circle size was 1° or 2° , duration thresholds did not differ systematically. However, duration thresholds have increased significantly from 5° to 12° annular gratings in both contrast levels, due to suppression.

3.2 Divisive Normalization Model

For our divisive normalization simulations, we have looked for whether its simulated duration thresholds using V1 and MT parameters in both model approaches (winner-take-all and population summation) is consistent with our behavioral

data. We have ran simulations for each stimulus size and contrast across stimulus types and used Eq. 1.3 to find simulated duration thresholds.

Overall, via function fitting, we observed that simulated duration thresholds of the same stimuli are consistent with behavioral data for both model approaches for both contrast levels (pairwise comparisons, mean of four R^2 values were .91), when MT parameters are used (Figure 3.7 and 3.8). In these figures, we observed that divisive normalization models were able to simulate facilitative and suppressive effects we saw in our behavioral data successfully. We expected that MT models would better predict duration thresholds from our behavioral experiment in these simulations. This was also consistent with previous research indicating that MT is the source region for the surround modulation mechanisms to occur when stimuli varying in size and contrast were measured in duration thresholds.

In both model approaches, simulations ran with parameters from literature for V1 have failed to show patterns we expect to see in terms of surround modulation mechanism effects (i.e. facilitation and suppression). This is reversed in the simulations we ran in which we used parameters for MT region from literature. This also suggests that using parameters for MT region is a better fit to behavioral data.

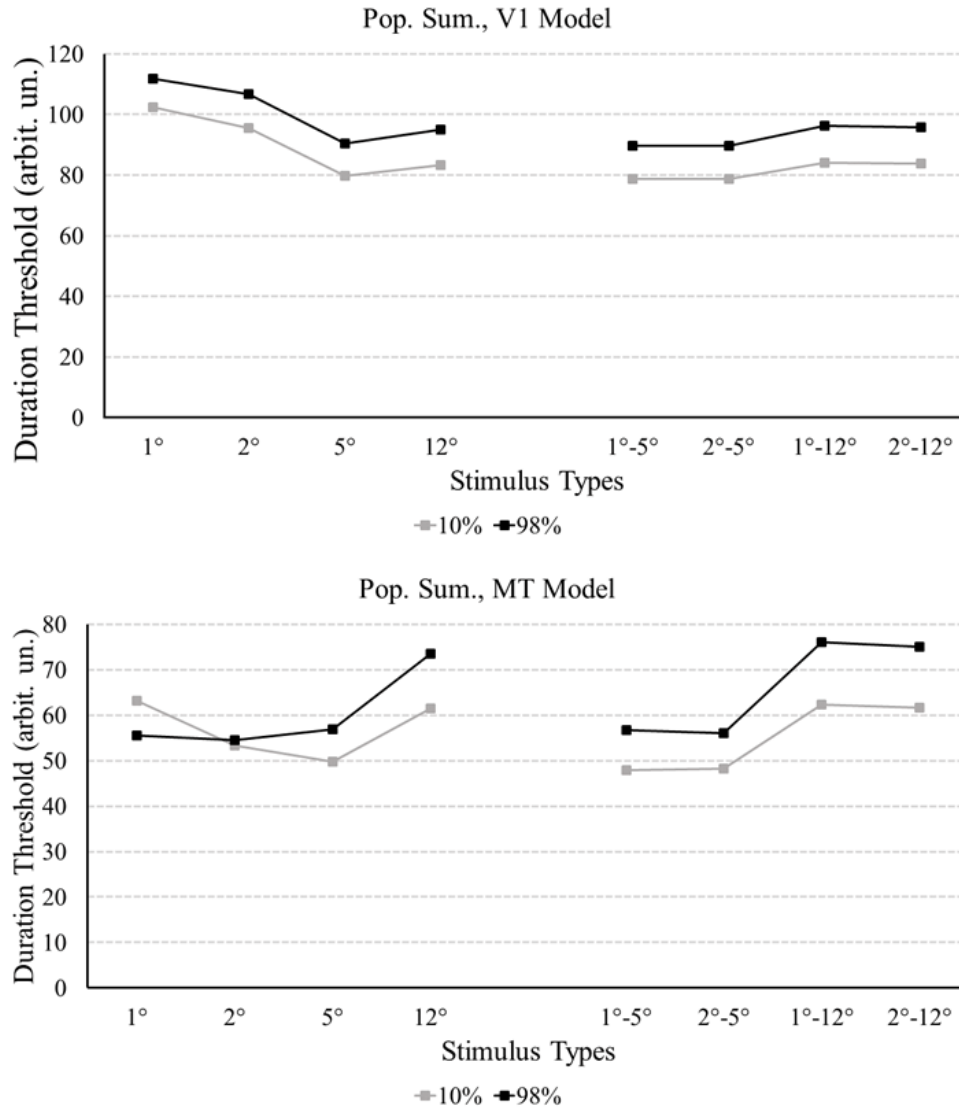


Figure 3.7: Simulated motion discrimination threshold (arbitrary units) changes between different stimulus sizes (degrees) and contrasts (percent) using V1 and MT parameters in population summation approach. First four in disc gratings (1°, 2°, 5°, 12°), last four annular gratings (1°-5°, 2°-5°, 1°-12°, 2°-12°).

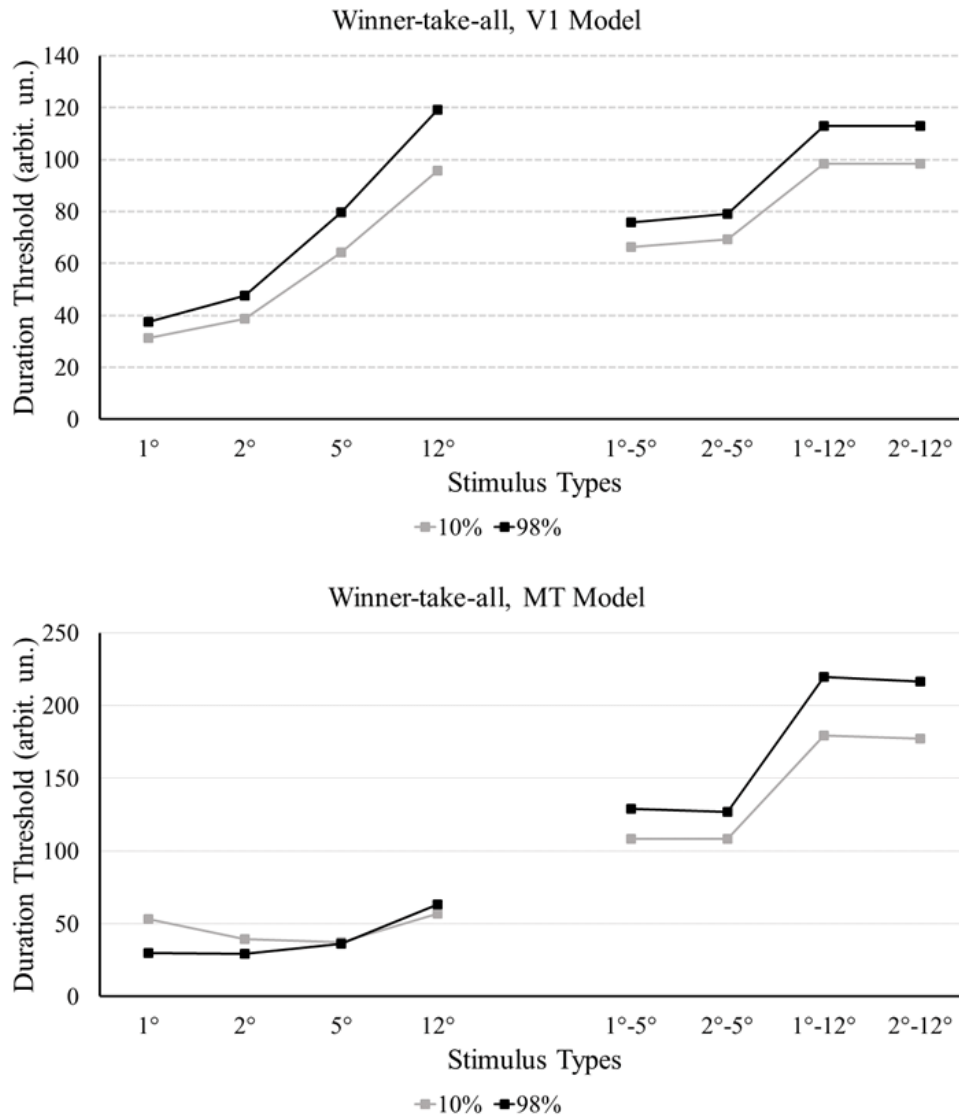


Figure 3.8: Simulated motion discrimination threshold (arbitrary units) changes between different stimulus sizes (degrees) and contrasts (percent) using V1 and MT parameters in winner-take-all approach. First four in disc gratings (1°, 2°, 5°, 12°), last four annular gratings (1°-5°, 2°-5°, 1°-12°, 2°-12°).

Chapter 4

Discussion

For this thesis, we tried to tackle how behavioral responses to drifting stimuli change taking a tripartite approach using drifting small disc, annular, and large disc grating stimuli; and how this information processing may show some possible pooling properties within brain areas processing motion direction perception. As many aspects of vision, motion discrimination processes were also employed with center-surround antagonistic features, we have decided to implement annular grating stimuli in our research, too. This implementation was missing from the literature and would be a crucial next step in explaining surround modulation effects in motion discrimination in a more systematic manner. Although we may not be able to derive causal relationships between how different parts of a receptive field process motion information with our behavioral results, we believe that this study would be a gateway to understand possible pooling properties within and between classical and surround receptive field. Hence, using small disc, annular, and large disc gratings to measure motion discrimination thresholds could give us an idea of how these parts of RFs pool information whether it be in itself or between upper regions in motion processing hierarchy. This was how we decided to do a behavioral study to investigate these research questions on pooling properties.

We derived three different regimes of pooling: Efficient, and inefficient (weak

and strong suppression) pooling (Figure 3.1). These three pooling properties would cover most of the probabilities regarding motion discrimination processing. First one, would suggest a facilitative effect when moving from small disc and annular grating to large disc grating. Therefore, we would expect a decrease in duration thresholds to large disc grating compared to small disc and annular gratings in our behavioral data. Secondly, a weak suppression regime would be the case that the duration threshold of large disc grating being in between of small disc and annular grating duration thresholds. This could suggest us that while cRF and sRF are processing small disc and annular grating, there would be a suppression, since center-surround portions of an RF would try to inhibit each other due to their antagonistic structure. Moreover, because visual information coming to the visual system carries the same type of information for both cRF and sRF, this similarity of neural image falling onto a single RF would therefore cause this conflict within cRF or sRF. Another possibility suggests that this suppressive effect may come from a higher-level decision area that pools information from multiple receptive fields. Hence, a strong suppression regime may indicate that the suppression may come from within an RF and between RF and upper layers as a result of this pooling of motion discrimination information. Because duration thresholds for large disc gratings would be greater than small disc and annular gratings for strong suppression regime, we might derive that suppression would come as a feedback from both within an RF and upper regions (Fig. 1.1).

To sum up, our behavioral experiment results have indicated that motion discrimination processes are mainly driven by inefficient pooling, namely, strong suppression. This means that while viewing these stimuli changing in size and contrast, duration thresholds of participants to large disc gratings were almost always greater than duration thresholds to small disc and annular gratings. This could mean that there is a nonlinearity in information pooling of drifting stimuli moving from small disc and annular to large disc gratings. Whereabouts of this suppression effect, as we mentioned above, cannot be driven by a single behavioral study. However, since duration thresholds of large disc gratings are greater than duration thresholds of other stimuli, this modulation effect may derive from both lateral connections between RF parts or between RF and higher-level decision

areas.

When we further investigate our behavioral data, we may see that our results are successful replicating results from the literature [71, 73, 92, 93]. We were able to capture facilitation and suppression effects due to changes in size and contrast in our stimuli. In contrast to other studies in literature we were also able to capture these modulatory effects of surround after implementing annular stimuli. As it may be observed in Figures 3.2 and 3.3, duration thresholds for discriminating motion direction in annular stimuli were almost always in between thresholds of small and large disc stimuli. This would suggest that it takes more effort to reach a final verdict on motion direction because of surround suppression, if annular stimuli is only processed by the surround portion of RFs specialized in motion discrimination. Since our annular stimuli was not small enough to be processed by a single RF in lower layers of the dorsal stream, only RFs in MT or higher-level regions could have big enough sRFs to process our annular gratings by themselves [52]. Therefore, if annular gratings are in fact processed by a single sRF and if this is the main reason we see an increase in duration thresholds from small disc, annular, to large disc grating; these sRFs then could be located in MT or regions as LIP, 7a, which are higher in hierarchy in dorsal stream.

In our divisive normalization model simulations, implementing small disc, annular, and large disc stimuli to divisive normalization models also allowed us to compare and contrast simulated duration thresholds using both V1 and MT parameters from literature. As we introduced in the Methods section, these models are used to get sensitivity of an arbitrary neuronal population to a grating. To achieve this, excitatory kernel, which is representative of the stimulus drive evoked by viewing a grating is first convolved with the neuronal image of our stimuli (Eq. 2.2). This convolution gave us the excitatory drive, which is then convolved with the suppression kernel to get suppressive drive (Eq. 2.3). These excitatory and suppressive drives are then divided to find the overall response (Eq. 2.1). Since sensitivities and thresholds are negatively related, decreased sensitivities suggested greater suppression than excitation because suppressive drive is in denominator.

We utilized these simulations to see whether these behavioral responses are more consistent with simulated thresholds ran with V1 or MT parameters. Divisive normalization model simulations successfully predict the behavioral results at a qualitative level. These simulations of duration thresholds from predicted neuronal response to all of our stimuli was most consistent with the parameters used for predicting MT response in both model approaches. This means that we were also able to get similar patterns of facilitation and suppression in simulated motion discrimination thresholds, as our behavioral data.

In terms of simulated duration threshold patterns, implementing MT parameters to winner-take-all model was more suiting to behavioral data at a quantitative level than population summation approach because of low contrast thresholds for disc gratings were greater than high contrast ones. These results were also in line with previous literature because of how these two model approaches are used to calculate overall response to the same stimulus. Population summation approach, as mentioned in Introduction section, computes the summed response of a portion of neuronal population that is centered to a stimulus. Therefore, with this method, we obtain a predicted response from the most active parts of that population, along with negative response. This approach then allows us to have a general idea of the balance between suppression and facilitation factors playing a role as stated in Er and his colleagues (2020). Yet, the winner-take-all assumption only takes the response of the most sensitive neuron into account, via taking the greatest response created by that arbitrary neuronal population as the final response. Hence, this approach enables us to assume for cRF response, since that will be the most sensitive. Taking these into consideration, it is only logical that we observe consistencies between population summation simulations using MT parameters and MT BOLD responses, as previous research have shown [93]. Recent studies have also shown that behavioral responses to drifting grating stimuli was similar to winner-take-all simulations using MT parameters [92] due to the peak response selection.

In conclusion, differences in duration thresholds of different types of stimuli showed strong suppressive properties, when we compared duration thresholds of

small disc, annular, and large disc drifting stimuli. This was consistent with previous research showing nonlinearities in processing different stimuli in terms of motion direction. Meaning that, we were able to observe facilitative and suppressive changes in motion discrimination thresholds of different stimuli changing in size and contrast. However, when we implemented an annular grating and compared to small and large disc stimuli, which have the same sizes as annular grating; we observed that inefficient pooling was prominent, namely, strong suppression. In divisive normalization model simulations, we observed simulated duration threshold patterns using MT parameters were more similar to behavioral data.

4.1 Limitations

Although our results were very much in line with the previous literature, what we discovered was that there was strong suppression pooling between almost every small discs-annular-large disc triples. This could be due to how we created neural images of annular gratings or possibly due to attentional field size of participants. For simulations of annular grating thresholds, we have created a neural image for annular gratings via considering two different mean values (μ) as explained in Figure 2.3 on only one dimension of an annulus. Therefore, while creating an annular stimuli, changes should be made in a two-dimensional plane in order to simulate response for annular stimuli. Since model simulations were also a secondary tool, we only used those simulations to see whether our behavioral results were consistent using which of the parameter sets used for V1 and MT brain regions. Therefore, if there is a way for a rigorous computation method to implement annular stimuli, it should be used to yield more realistic results.

Secondly, for this study, we did not control for attentional field size, which is known to change the surround modulation mechanisms [88]. Attentional focus and target stimuli are known to have an effect on suppression strength according to these recent studies. When attentional field is narrowed and does not include the target stimulus, researchers have observed that suppression effect on response

evoked by that stimulus is weakened. On the other hand, when attention is expanded to cover the stimulus and directed onto the target stimulus, suppression effect goes back its to normal level. Owing to the fact that we did not manipulate or have given any direction to participants other than fixing their eyes onto the fixation point, could have a systematic effect on behavioral duration thresholds. Meaning that, all participants could have extended their attentional fields to cover the stimulus appearing on the screen and this could be the reason for the strong suppression effect we saw in our behavioral experiment results. Moreover, because there was no manipulation of attention in our behavioral study, as well as we did not introduce an attentional drive to our divisive normalization model. By not introducing this additional parameter into the equations of our model, the model automatically assumes an attentional drive that is equally distributed to the visual field, or in this case, neuronal population.

Finally, another limitation to this study is that we provide little to no evidence on anatomical implications to feedback and feedforward connections outside of our range of pooling regimes. We have speculated that these surround modulation effect could be coming from MT, since it is the region to use facilitatory and suppressive mechanisms to further understand the visual field [64, 100]. However, we may never be sure if these surround modulatory effects would undeniably come from MT region, with the experiments we conducted for this thesis. Therefore, origin of these suppressive effects we observed between different types of stimuli could emerge from MT and extend to areas as lateral intraparietal area (LIP), 7a in superior parietal lobe (SPL) [1]. Conclusively, without a study addressing the anatomical implications of these feedback and feedforward connections, we may not be able to say from where the suppression effect is coming from.

4.2 Implications

Visual system depend on surround modulation mechanisms in cases where ambiguity and therefore reliability of visual information varies. When information coming from outside is ambiguous or not reliable, surrounding regions facilitate

the activation caused by the non-reliable stimulus, to gather all information related to that stimulus as much as possible. This creates the facilitation effect caused by the surround, which increases the sensitivity to that particular stimulus. In this way, because overall activation is increased, we are quicker in detecting motion direction of that stimulus. This facilitative state is usually achieved via low contrast drifting stimuli in motion perception. Oppositely, when we view a non-ambiguous stimulus, we have reliable information coming through the visual system. In cases where there is more information than needed, there is probably an overload of that information. For an efficiently working system, surround portions of receptive fields processing that drifting grating suppresses the center portion, inhibiting the excess information. In this sense, these modulation mechanisms work in such a way that there is sufficient information for us to determine the direction of motion in our visual field. For instance, let us assume that we record space from Earth over a period of time to find out Earth's orbit and watch the recording at a higher speed. Considering that Earth orbits around Sun, stars and planets further away from Earth is viewed more stationary than the closer ones. Therefore when we observe the space, some stars and planets closer to Earth will move in various directions. Ones that are further away will move consistently to each other, creating a global motion. If we have a low resolution recording, surround modulation mechanisms will facilitate our perception creating more activation and we will detect overall motion or orbit of the Earth faster. However if the recording is high in resolution, we may detect this motion a little slower.

These modulation mechanisms present itself in human brain as excitatory and inhibitory connections. Excitation-inhibition imbalance (E/I imbalance) within human brain is known to play a major role to many neurocognitive disorders such as schizophrenia, bipolar, autism spectrum disorders [106, 107, 108]. These imbalances are mainly caused by disfunction of a certain brain region or excessive amounts of a neurotransmitter. This imbalance tend to reveal itself via various symptoms, weak suppression being one of the core ones. Weak suppression in individuals with these disorders may also present itself in motion discrimination

perception. Researchers have observed that these individuals have weakened suppressive responses, which also shows itself while viewing visual stimuli, such as poorly suppressed responses or decreased duration thresholds to high contrast grating stimuli in schizophrenia patients, heightened ability to see low-level details in autism spectrum disorders [109, 110, 111, 112, 113]. Hence, understanding E/I balances within the visual system utilizing motion perception while looking at pooling efficiency in different settings may help us better understand these disorders, too.

4.3 Future Directions

As we mentioned in Limitations section, attentional field size and its manipulation may introduce a key variable into how response pooling works of motion perception. Behaviorally narrowing and widening the attentional field in human participants could change motion discrimination thresholds, as well as provide additional information on how surround modulation systems work. This manipulation could be done in all steps of our research by implementing an attention condition behavioral experiment and divisive normalization models, in addition to future fMRI experiments. Looking at brain imaging studies combined with populational summation models would allow us to compare and contrast how responses to these stimuli change after addition of this condition. Asking participants to only focus on a fixation point or asking them to report the motion direction of a stimulus would suffice in terms of manipulating their attentional field by narrowing and widening it. This could be done via simultaneously showing a fixation point and a drifting grating stimulus. Fixation tasks are generally based on reports of color change in a fixation dot done by a key-press. Because this color change is quick and randomized in terms of its onset, this task allows researchers to ensure participant's full engagement to the experiment, resulting in a narrow attentional field. On the contrary, having participants to report only the motion direction of a stimulus automatically would expand their attentional field from the fixation point to stimulus size, resulting in a wide attentional field.

In conclusion, by implementing an attention condition to behavioral and brain imaging studies along with divisive normalization models would be the most important next step to understand which factors play a role in further characterization of surround modulation mechanisms. This will allow future researchers to see population-level responses that we could not obtain given the nature of our experiments and overall responses to the same stimuli could be manipulated more easily after implementation of attention.

4.4 Conclusion

Our study on characterization of surround modulation in motion discrimination perception showed that there was an increase in duration thresholds from small disc and annular grating to large disc gratings at both low and high contrast levels. Hence, among our three possible regimes of pooling, we observed strong suppression, which was a form of inefficient pooling. Divisive normalization model simulations also showed that using MT parameters from literature resulted in a similar pattern of duration threshold levels. This could also suggest that the suppression effect we observe in our behavioral data may emerge from MT region. However, by manipulating surround modulation effects more effectively, a brain imaging or anatomical study could further reveal underlying effects of these mechanisms.

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Appendix A

Behavioral Experiment

A.1 Psychometric Data Fitting

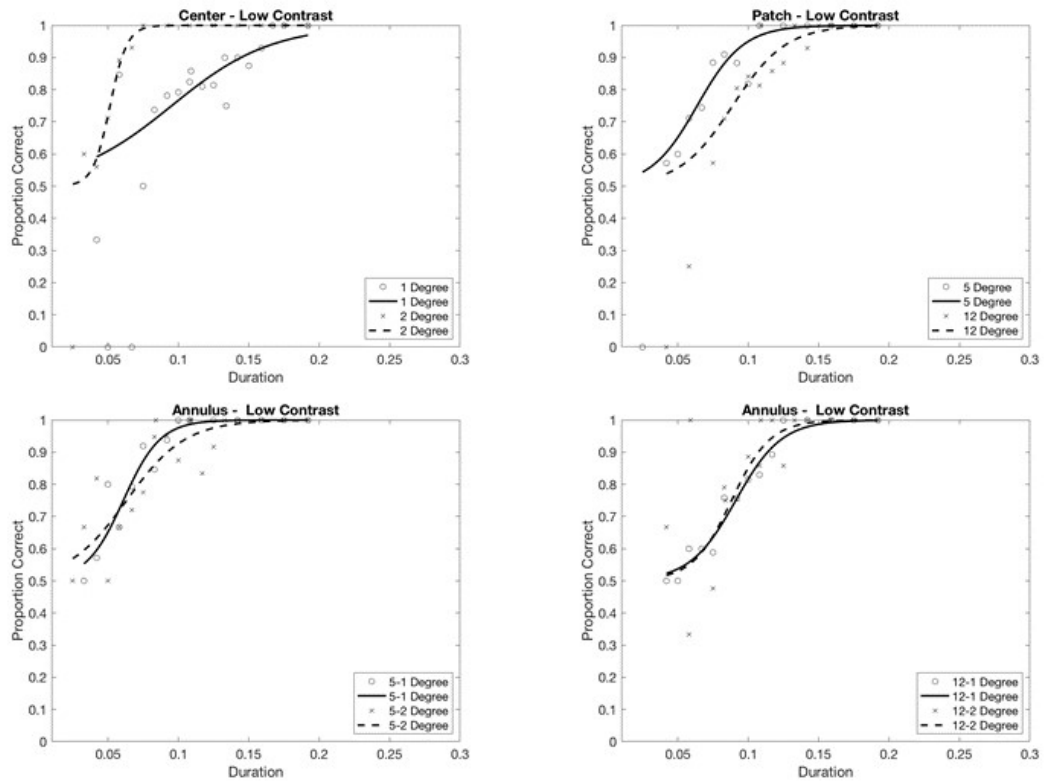


Figure A.1: Participant 1, low contrast: Duration threshold for 1° (73.4 ms, SE: 0.008), 2° (45.8 ms, SE: 0.006), 5° (59.9 ms, SE: 0.008), and 12° (82.9 ms, SE: 0.006) disc gratings and 1°-5° (47.1 ms, SE: 0.007), 2°-5° (55.9 ms, SE: 0.006), 1°-12° (79.1 ms, SE: 0.005), and 2°-12° (81.3 ms, SE: 0.006) annular gratings

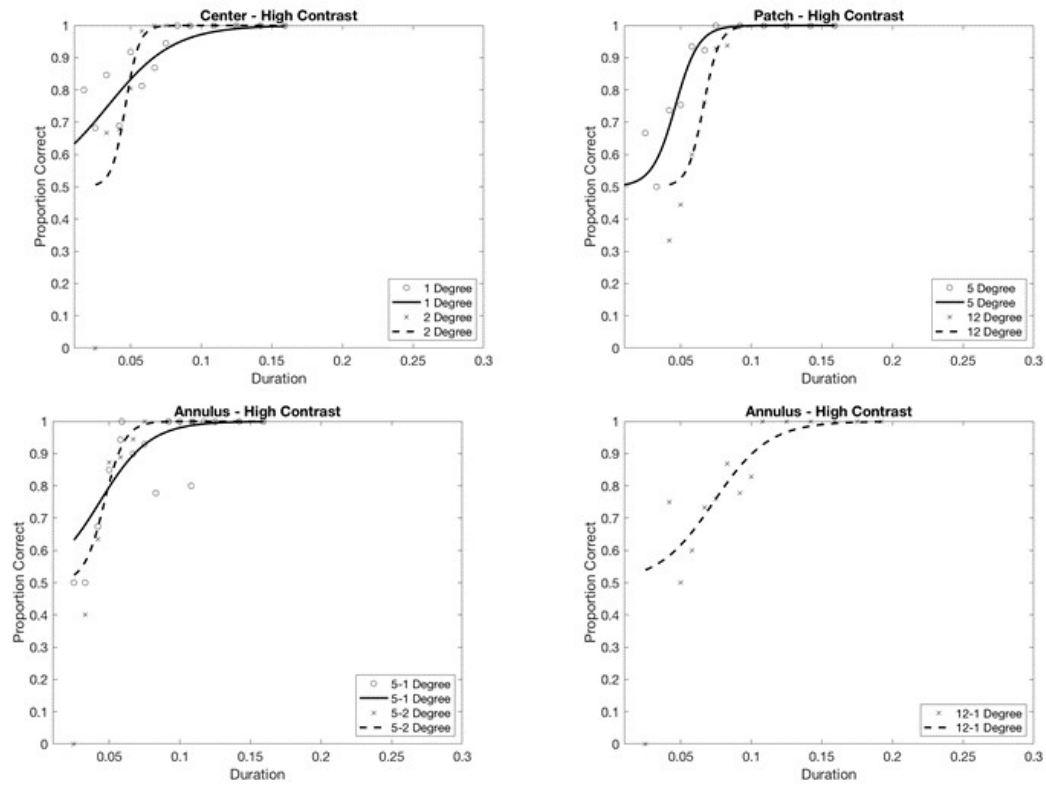


Figure A.2: Participant 1, high contrast: Duration threshold for 1° (33.8 ms, SE: 0.014), 2° (46.3 ms, SE: 0.001), 5° (46.2 ms, SE: 0.003), and 12° (66.1 ms, SE: 0.002) disc gratings and 1°-5° (43.2 ms, SE: 0.005), 2°-5° (46.6 ms, SE: 0.002), 1°-12° (59.3 ms, SE: 0.017), and 2°-12° (68.6 ms, SE: 0.007) annular gratings

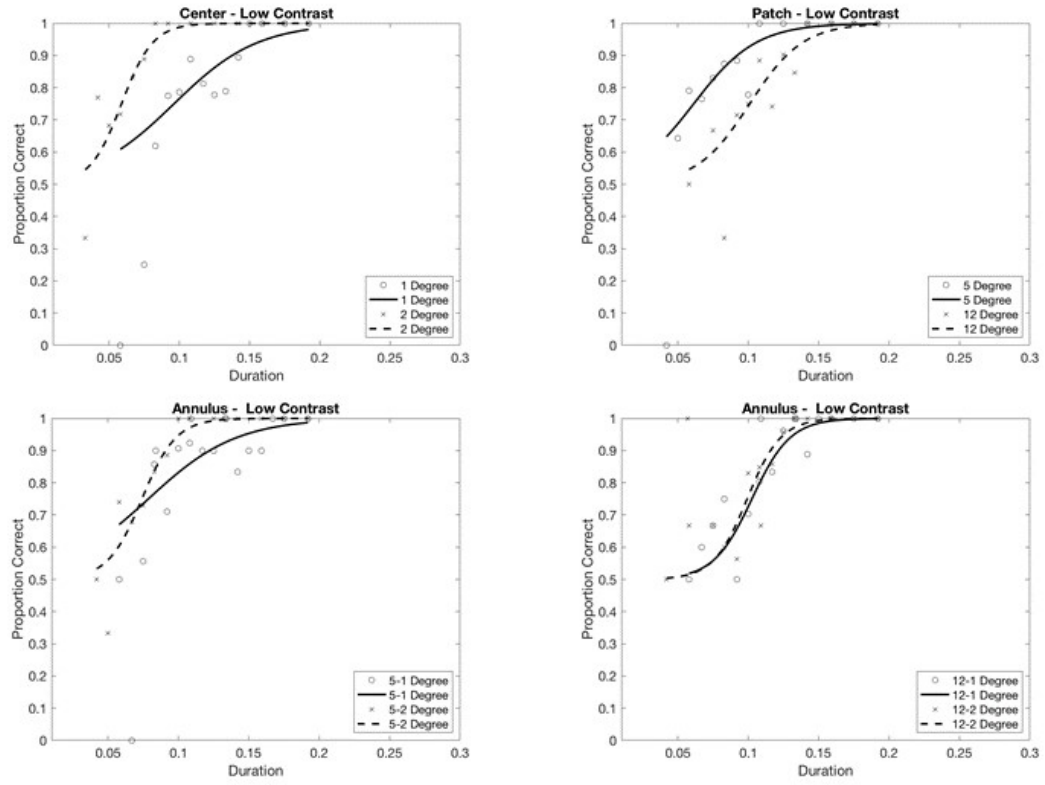


Figure A.3: Participant 2, low contrast: Duration threshold for 1° (96.2 ms, SE: 0.017), 2° (58.8 ms, SE: 0.004), 5° (61.3 ms, SE: 0.008), and 12° (101.1 ms, SE: 0.006) disc gratings and 1°-5° (78.7 ms, SE: 0.014), 2°-5° (74.1 ms, SE: 0.004), 1°-12° (102.6 ms, SE: 0.005), and 2°-12° (99.3 ms, SE: 0.004) annular gratings

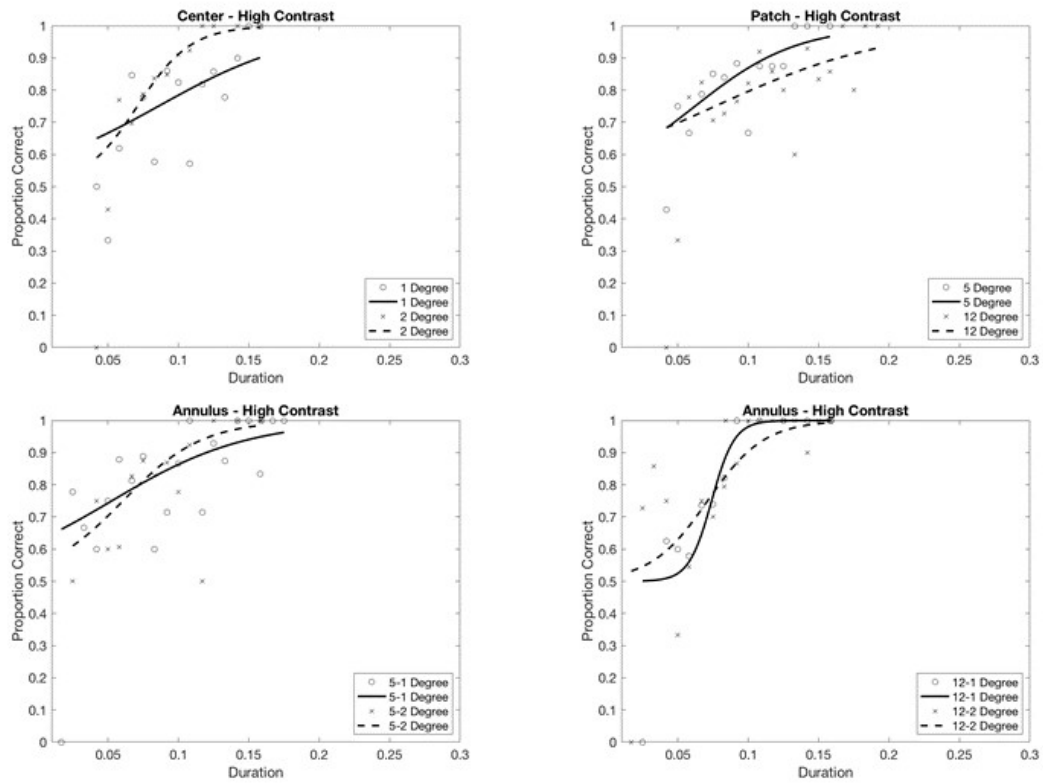


Figure A.4: Participant 2, high contrast: Duration threshold for 1° (85.8 ms, SE: 0.015), 2° (70.9 ms, SE: 0.006), 5° (62.2 ms, SE: 0.022), and 12° (76.5 ms, SE: 0.018) disc gratings and 1° - 5° (52.7 ms, SE: 0.018), 2° - 5° (60.6 ms, SE: 0.012), 1° - 12° (74.0 ms, SE: 0.003), and 2° - 12° (71.1 ms, SE: 0.007) annular gratings

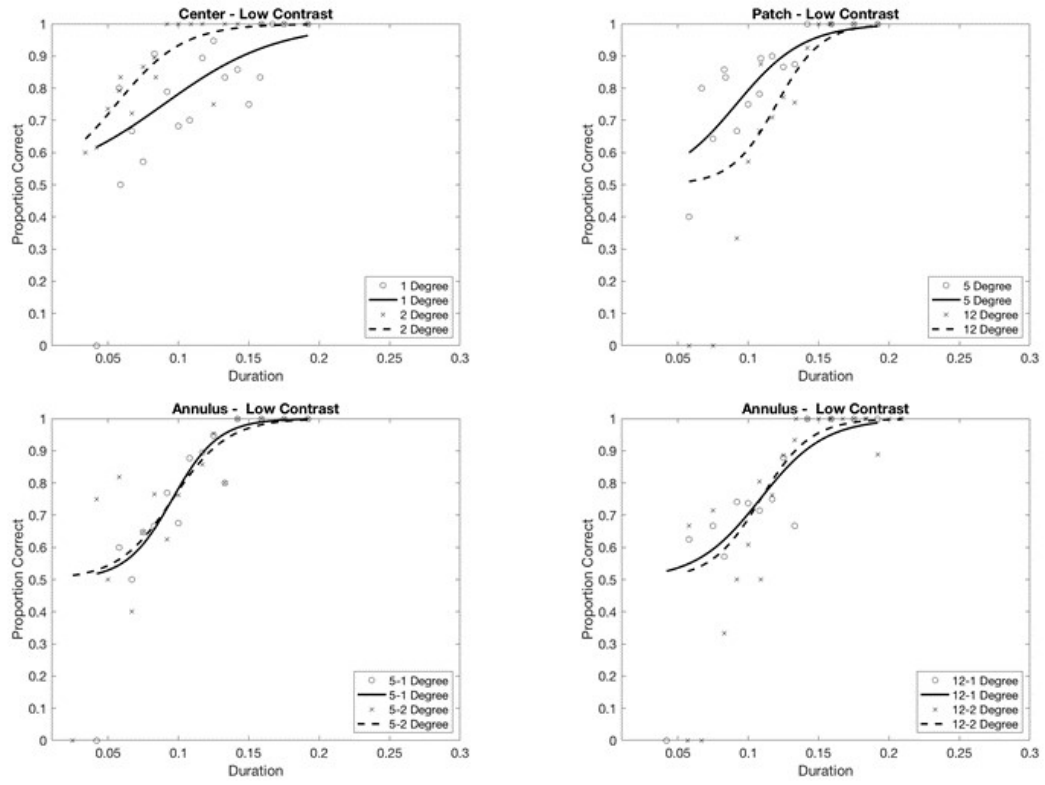


Figure A.5: Participant 3, low contrast: Duration threshold for 1° (89.7 ms, SE: 0.024), 2° (55.9 ms, SE: 0.008), 5° (91.5 ms, SE: 0.008), and 12° (120.1 ms, SE: 0.006) disc gratings and 1°-5° (95.7 ms, SE: 0.005), 2°-5° (95.9 ms, SE: 0.006), 1°-12° (108.5 ms, SE: 0.007), and 2°-12° (108.8 ms, SE: 0.005) annular gratings

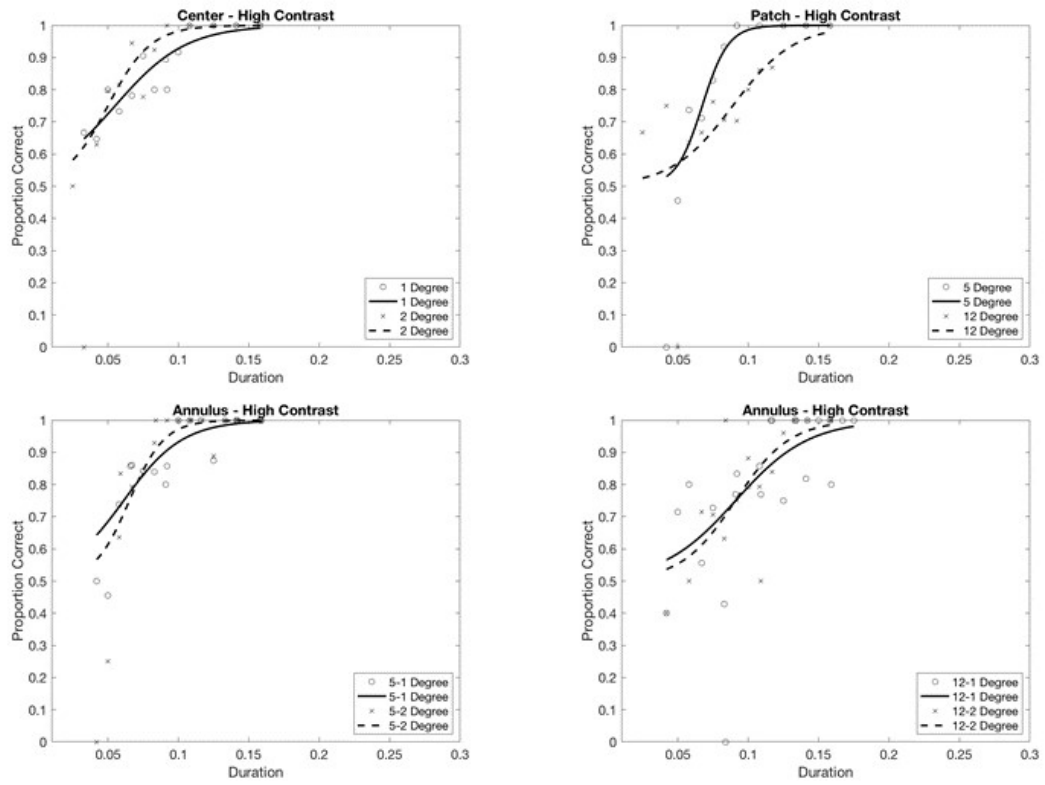


Figure A.6: Participant 3, high contrast: Duration threshold for 1° (55.1 ms, SE: 0.011), 2° (50.0 ms, SE: 0.005), 5° (67.4 ms, SE: 0.003), and 12° (89.0 ms, SE: 0.007) disc gratings and 1°-5° (61.2 ms, SE: 0.007), 2°-5° (65.2 ms, SE: 0.004), 1°-12° (91.0 ms, SE: 0.009), and 2°-12° (90.9 ms, SE: 0.006) annular gratings

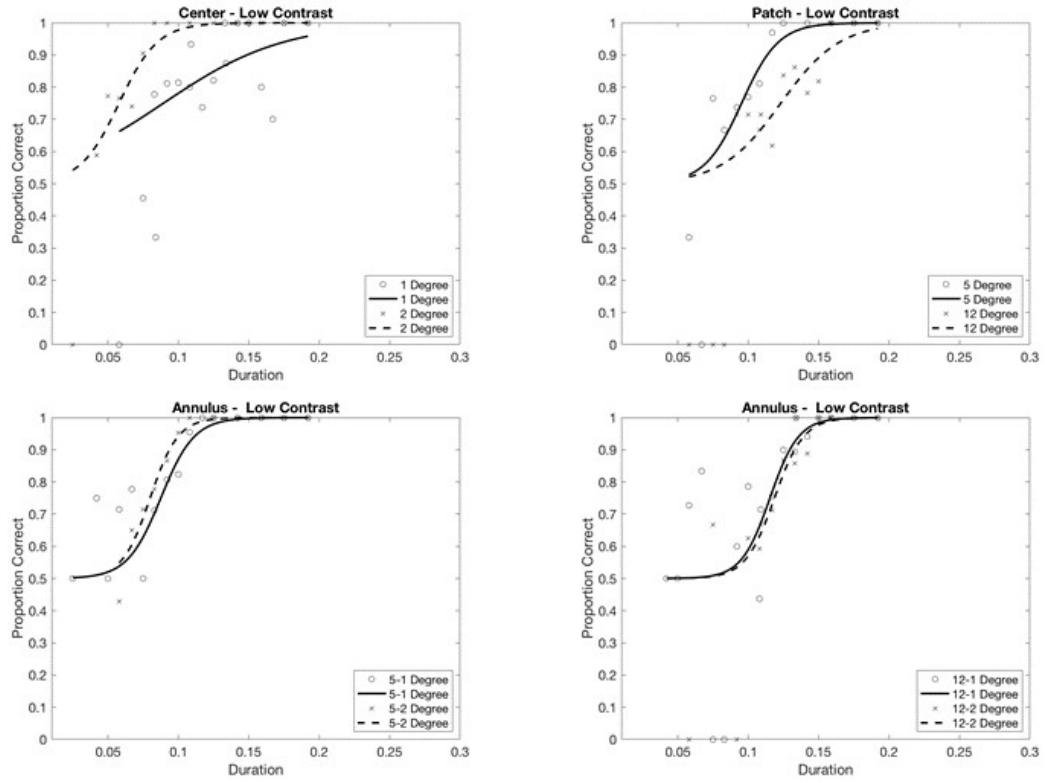


Figure A.7: Participant 4, low contrast: Duration threshold for 1° (89.3 ms, SE: 0.086), 2° (57.9 ms, SE: 0.004), 5° (95.3 ms, SE: 0.004), and 12° (123.1 ms, SE: 0.007) disc gratings and 1°-5° (87.5 ms, SE: 0.003), 2°-5° (79.9 ms, SE: 0.003), 1°-12° (115.4 ms, SE: 0.003), and 2°-12° (118.6 ms, SE: 0.003) annular gratings

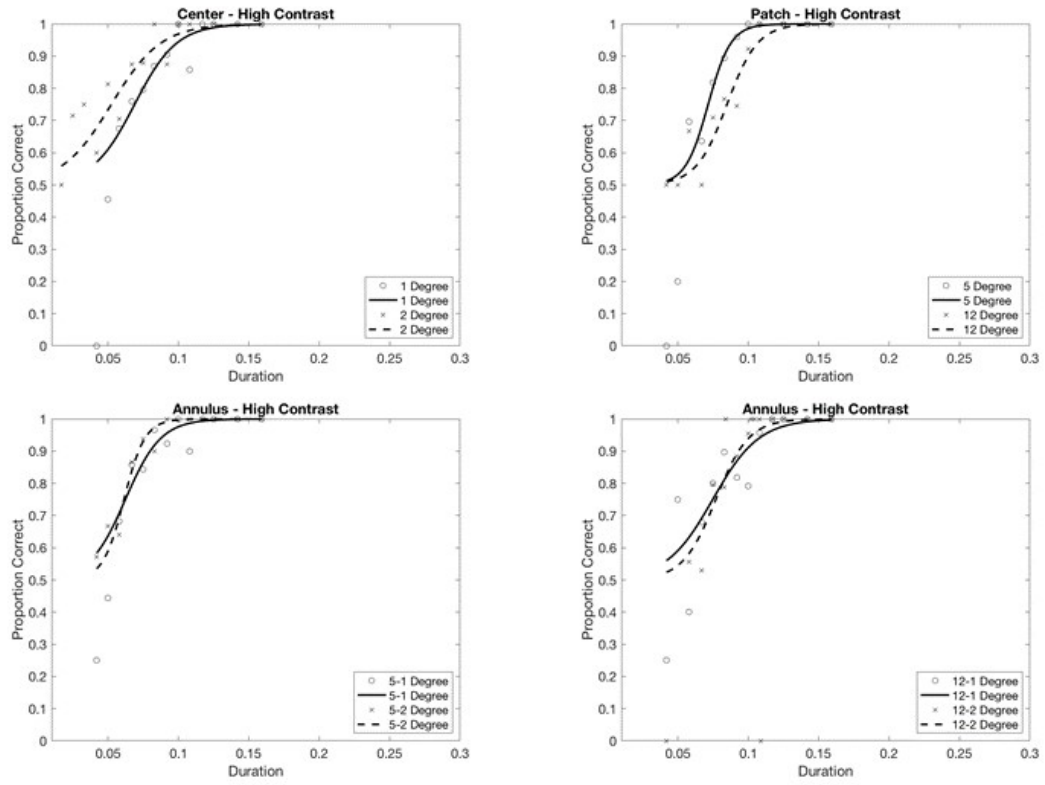


Figure A.8: Participant 4, high contrast: Duration threshold for 1° (68.9 ms, SE: 0.004), 2° (52.4 ms, SE: 0.006), 5° (71.6 ms, SE: 0.002), and 12° (84.6 ms, SE: 0.003) disc gratings and 1° - 5° (62.4 ms, SE: 0.004), 2° - 5° (61.4 ms, SE: 0.002), 1° - 12° (74.8 ms, SE: 0.005), and 2° - 12° (77.0 ms, SE: 0.004) annular gratings

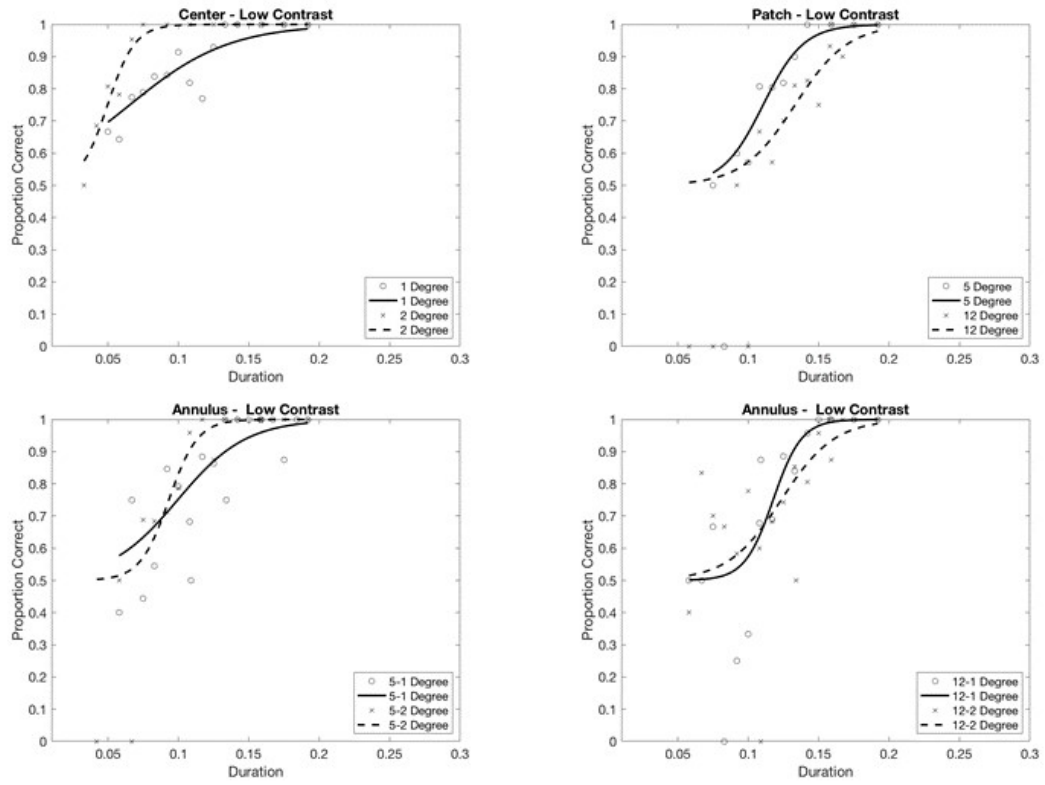


Figure A.9: Participant 5, low contrast: Duration threshold for 1° (65.5 ms, SE: 0.017), 2° (49.7 ms, SE: 0.003), 5° (110.6 ms, SE: 0.005), and 12° (133.3 ms, SE: 0.007) disc gratings and 1° - 5° (99.5 ms, SE: 0.008), 2° - 5° (93.2 ms, SE: 0.004), 1° - 12° (117.2 ms, SE: 0.003), and 2° - 12° (123.4 ms, SE: 0.006) annular gratings

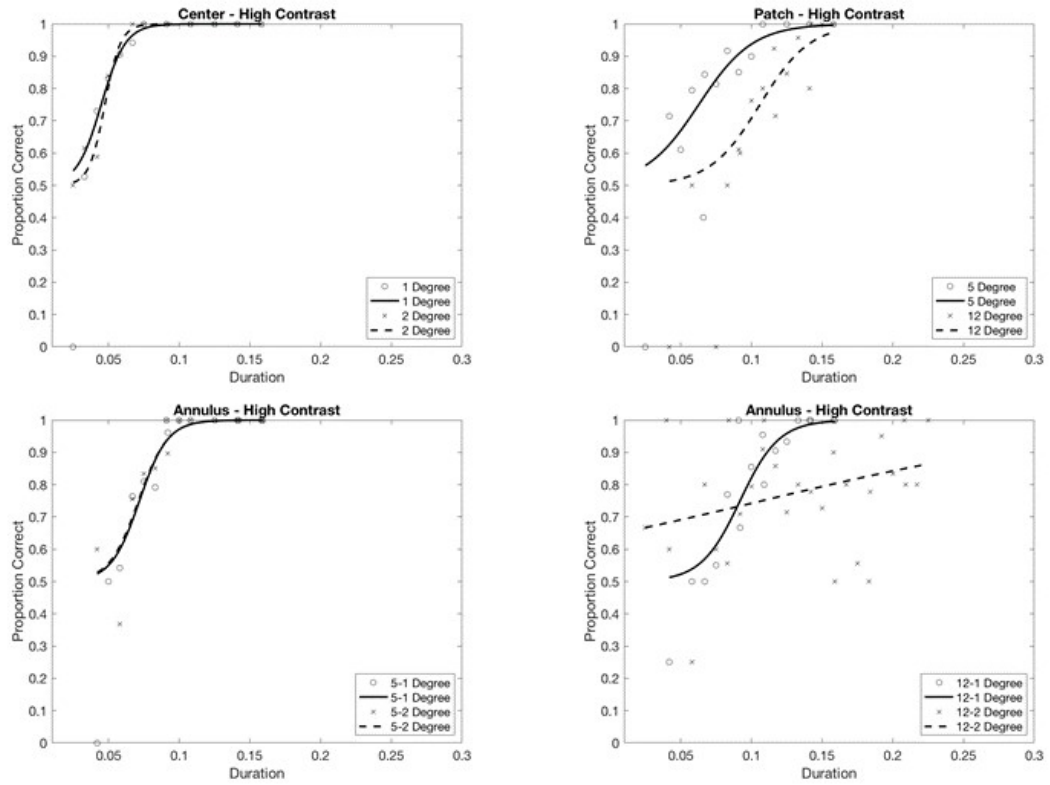


Figure A.10: Participant 5, high contrast: Duration threshold for 1° (44.9 ms, SE: 0.003), 2° (47.4 ms, SE: 0.002), 5° (62.7 ms, SE: 0.007), and 12° (106.0 ms, SE: 0.006) disc gratings and 1°-5° (71.9 ms, SE: 0.003), 2°-5° (71.1 ms, SE: 0.003), 1°-12° (92.0 ms, SE: 0.004), and 2°-12° (107.4 ms, SE: 0.011) annular gratings

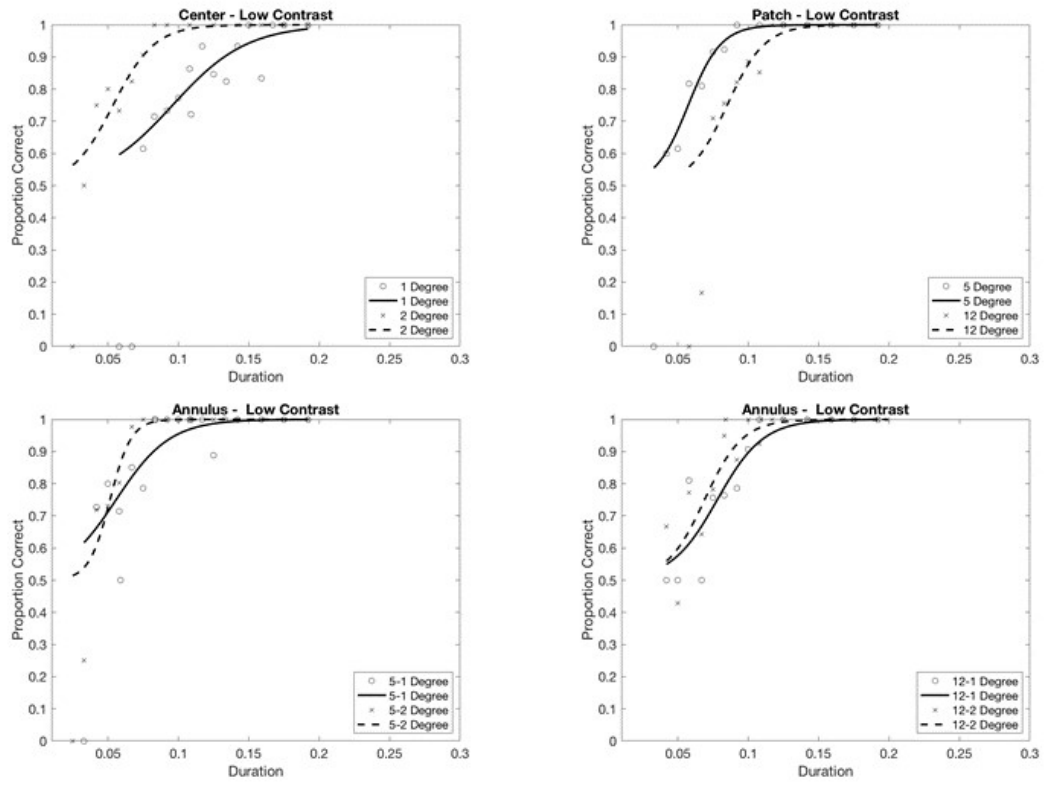


Figure A.11: Participant 6, low contrast: Duration threshold for 1° (95.0 ms, SE: 0.012), 2° (53.6 ms, SE: 0.005), 5° (57.4 ms, SE: 0.004), and 12° (85.0 ms, SE: 0.005) disc gratings and 1°-5° (55.8 ms, SE: 0.007), 2°-5° (51.4 ms, SE: 0.003), 1°-12° (78.0 ms, SE: 0.006), and 2°-12° (69.0 ms, SE: 0.004) annular gratings

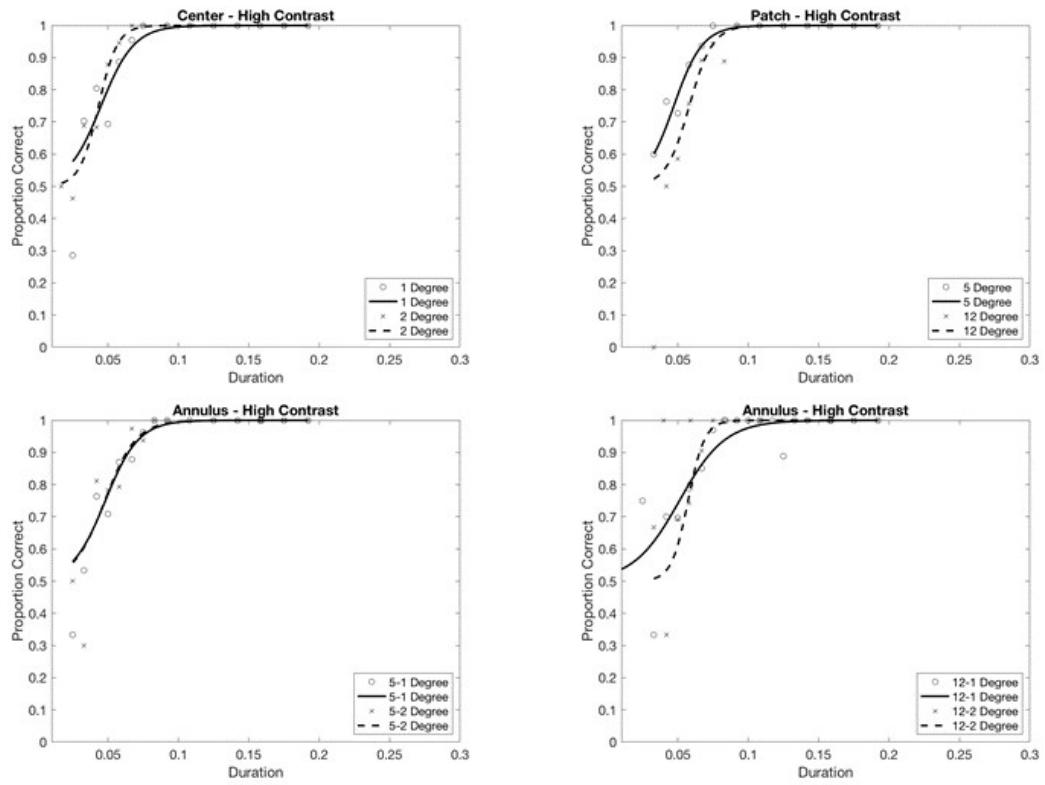


Figure A.12: Participant 6, high contrast: Duration threshold for 1° (45.0 ms, SE: 0.004), 2° (43.3 ms, SE: 0.002), 5° (47.2 ms, SE: 0.004), and 12° (58.2 ms, SE: 0.003) disc gratings and 1° - 5° (48.1 ms, SE: 0.004), 2° - 5° (47.7 ms, SE: 0.004), 1° - 12° (51.2 ms, SE: 0.006), and 2° - 12° (57.9 ms, SE: 0.002) annular gratings

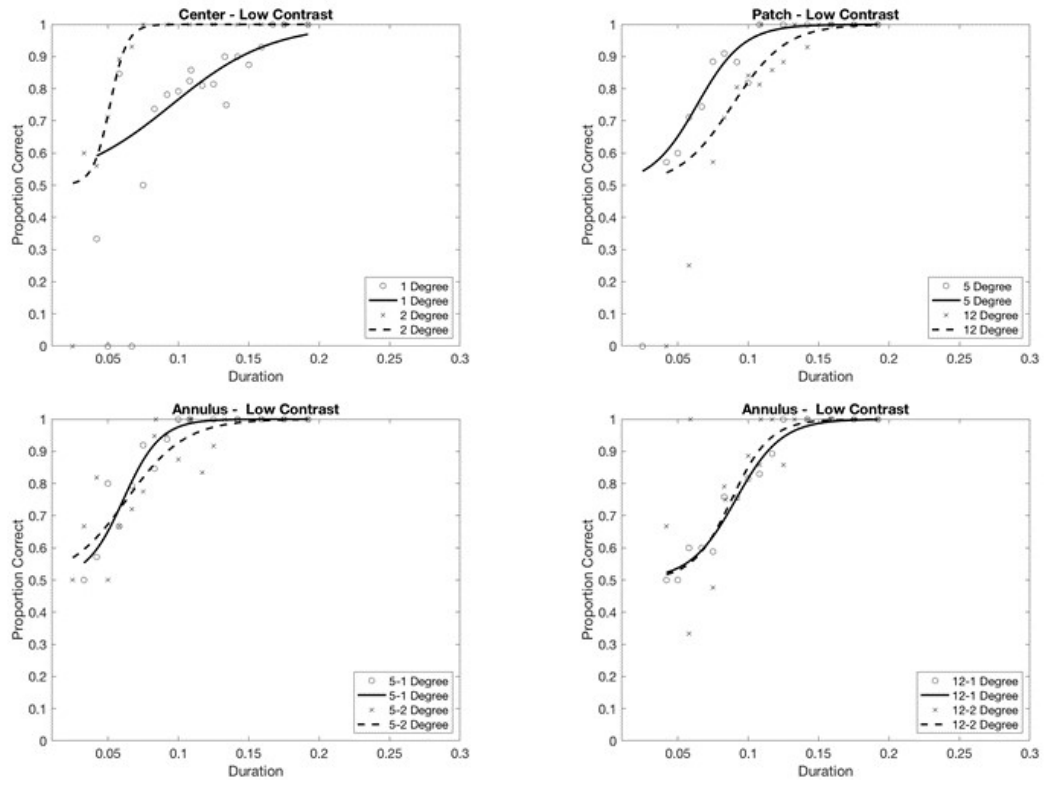


Figure A.13: Participant 7, low contrast: Duration threshold for 1° (95.2 ms, SE: 0.017), 2° (51.4 ms, SE: 0.002), 5° (63.7 ms, SE: 0.005), and 12° (88.9 ms, SE: 0.007) disc gratings and 1° - 5° (60.9 ms, SE: 0.004), 2° - 5° (63.2 ms, SE: 0.008), 1° - 12° (91.2 ms, SE: 0.006), and 2° - 12° (88.2 ms, SE: 0.004) annular gratings

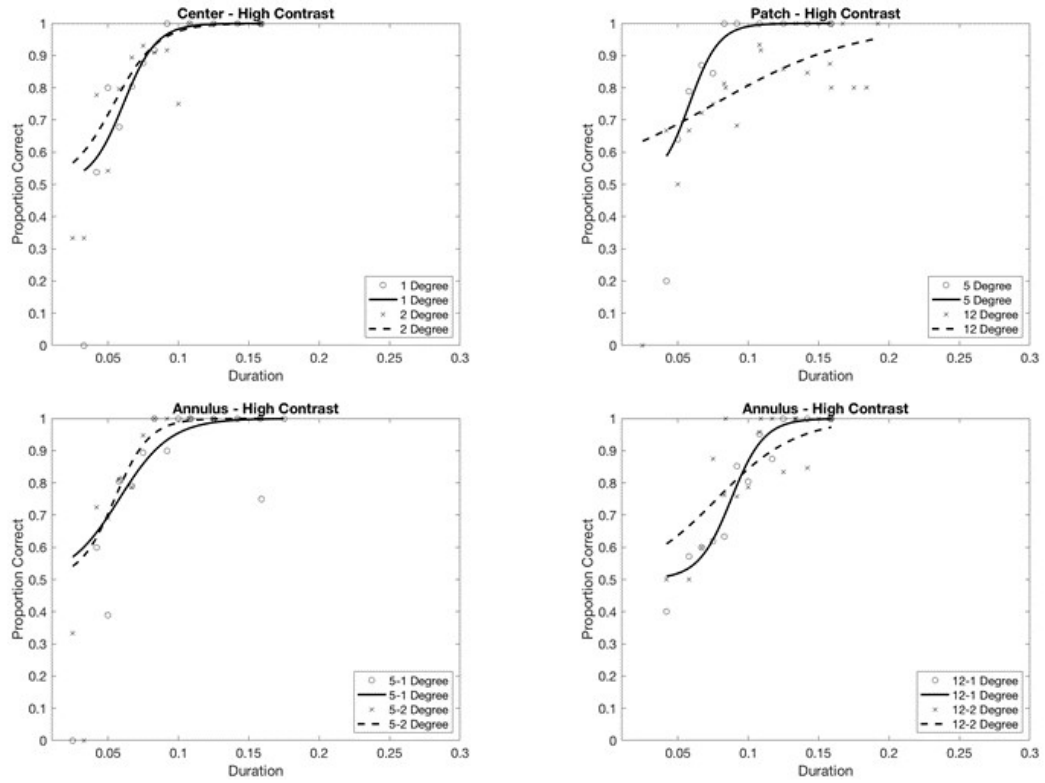


Figure A.14: Participant 7, high contrast: Duration threshold for 1° (60.9 ms, SE: 0.004), 2° (54.1 ms, SE: 0.005), 5° (58.3 ms, SE: 0.004), and 12° (76.1 ms, SE: 0.024) disc gratings and 1°-5° (58.0 ms, SE: 0.007), 2°-5° (54.7 ms, SE: 0.004), 1°-12° (88.0 ms, SE: 0.004), and 2°-12° (77.7 ms, SE: 0.010) annular gratings

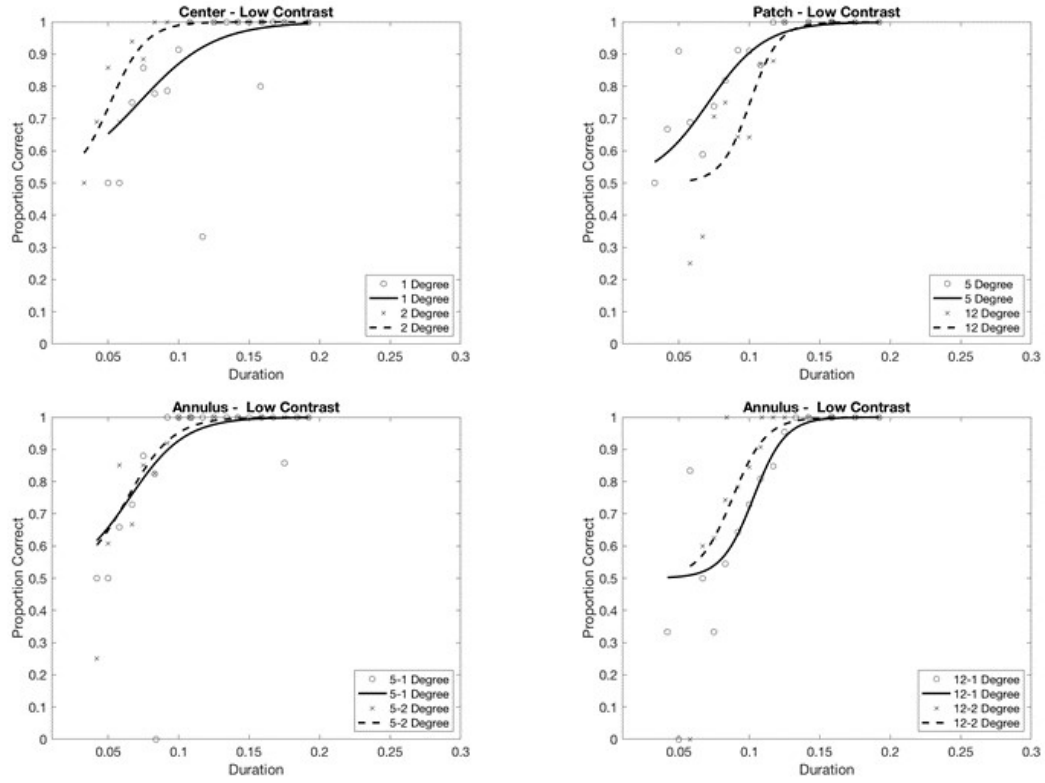


Figure A.15: Participant 8, low contrast: Duration threshold for 1° (72.0 ms, SE: 0.009), 2° (51.7 ms, SE: 0.005), 5° (71.1 ms, SE: 0.007), and 12° (105.5 ms, SE: 0.004) disc gratings and 1° - 5° (65.3 ms, SE: 0.006), 2° - 5° (63.8 ms, SE: 0.006), 1° - 12° (103.0 ms, SE: 0.004), and 2° - 12° (88.2 ms, SE: 0.004) annular gratings

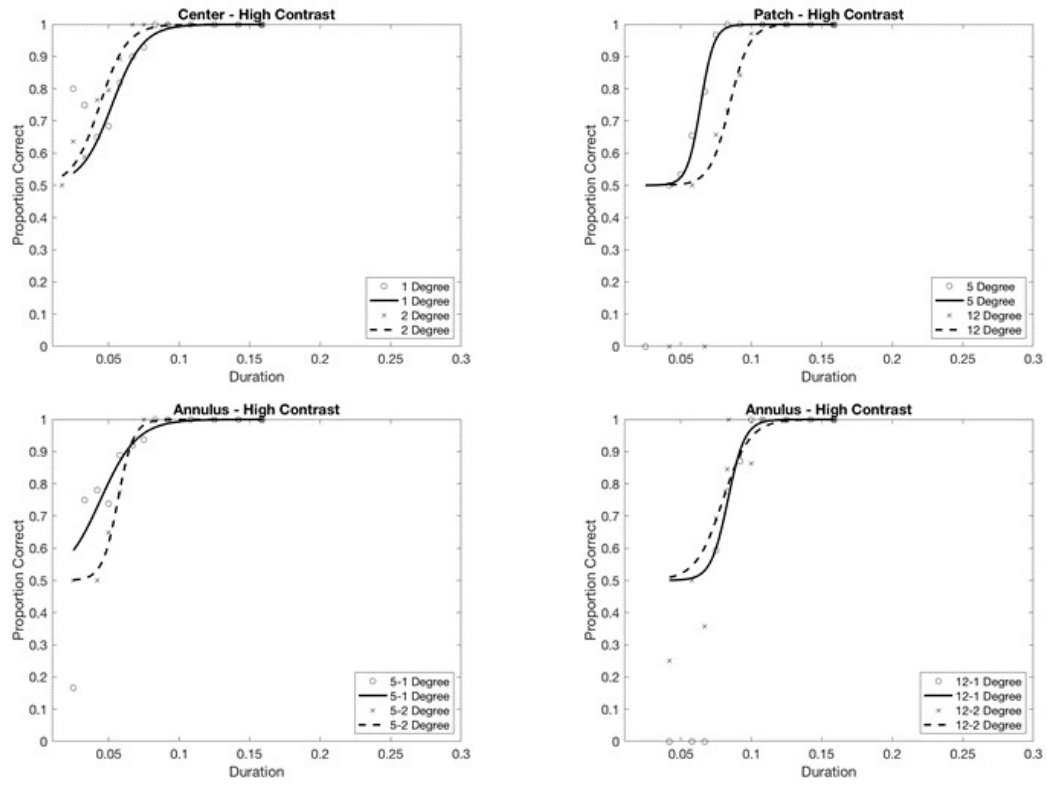


Figure A.16: Participant 8, high contrast: Duration threshold for 1° (52.4 ms, SE: 0.004), 2° (43.8 ms, SE: 0.004), 5° (64.1 ms, SE: 0.002), and 12° (84.7 ms, SE: 0.002) disc gratings and 1°-5° (44.5 ms, SE: 0.005), 2°-5° (56.6 ms, SE: 0.002), 1°-12° (83.4 ms, SE: 0.002), and 2°-12° (79.9 ms, SE: 0.003) annular gratings

Appendix B

Divisive Normalization Model

B.1 Codes

Listing B.1: Behavioral experiment

```
% Clear the workspace
close all; clear all;
fname=input('please write the name of the ...
participant\n','s');
Contrast = input('please write the contrast value\n','s');
Contrast = str2double(Contrast);
fname=[fname '.txt'];

% Setup PTB with some default values
PsychDefaultSetup(2);

% Seed the random number generator
rand('seed', sum(100 * clock));

% Screen Number
screenNumber = max(Screen('Screens'));
```

```

HideCursor;

% Define black, white and grey
white = WhiteIndex(screenNumber);
grey = 128/255;
black = BlackIndex(screenNumber);

% Open the screen
[window, windowRect] = PsychImaging('OpenWindow', ...
screenNumber, grey, [], 32, 2, [], [], ...
kPsychNeed32BPCFloat);
% Flip to clear
Screen('Flip', window);

% Open text file to write
fp = fopen(fname, 'w+');
fprintf(fp, '%15s\t%15s\t%15s\t%15s\t%15s\t%15s\t...
%15s\t%15s\t%15s\t%15s\t%15s\n', 'Trial', 'C. Size', ...
'P. Size', 'Cond', 'Staircond.', 'Contrast', ...
'Accuracy', 'RT', 'Duration', 'Etime');

% Set the text size
Screen('TextSize', window, 35);

% Query the frame duration
ifi = Screen('GetFlipInterval', window);
% Query the maximum priority level
topPriorityLevel = MaxPriority(window);

% scr.resolution = [1280 1024];
scr.scr_sizeX = 1280;
scr.scr_sizeY = 1024;
% scr.width = 1280;

```

```

scr.disp_sizeX = 310;
scr.disp_sizeY = 410;
scr.dist= 75;

% Get the centre coordinate of the window
[xCenter, yCenter] = RectCenter(windowRect);

% Set the blend function for the screen
Screen('BlendFunction', window, 'GLSRC_ALPHA', ...
'GLONE_MINUS_SRC_ALPHA');

% Keyboard information

escapeKey = KbName('!');
leftKey = KbName('LeftArrow');
rightKey = KbName('RightArrow');

% Condition Lists

% We are going to use contrast and annulus size

centerDegList= [0.5 1];
patchDegList= [2.5 6];
condList=[1];
for i=1: size(centerDegList,2)
    centerSizeList(1,i)=pixcalc((centerDegList(1,i)),scr);
end
for i=1: size(patchDegList,2)
    patchSizeList(1,i)=pixcalc((patchDegList(1,i)),scr);
end

% Number of trials per condition
trialsPerCondition = 120; %120

```

```

condMatrixBase = [108 108 108 260 108 260 108 260; ...
22 43 22 22 43 43 22 22; 1 1 2 2 2 2 3 3];

condMatrix = repmat(condMatrixBase,1, trialsPerCondition);
numTrials = size(condMatrix, 2);
shuffler = randperm(numTrials);
condMatrixShuffled = condMatrix(:, shuffler);

%staircase condition matrix
stair_cond = repmat([1 2], 1, numTrials/2);
stair_cond = Shuffle(stair_cond);
DriftdirectionList= repmat([-1 1], 1, numTrials/2);
DriftdirectionList = Shuffle(DriftdirectionList);

% Timing Information

low_init= ifi*7;
high_init= ifi*23;
initial_stepSize= ifi*2;

presTimeSecs_low_center_1= low_init;
presTimeSecs_low_center_2= low_init;
presTimeSecs_low_patch_1= low_init;
presTimeSecs_low_patch_2= low_init;
presTimeSecs_low_annulus_11= low_init;
presTimeSecs_low_annulus_21= low_init;
presTimeSecs_low_annulus_12= low_init;
presTimeSecs_low_annulus_22= low_init;

presTimeSecs_high_center_1= high_init;
presTimeSecs_high_center_2= high_init;
presTimeSecs_high_patch_1= high_init;
presTimeSecs_high_patch_2= high_init;

```

```

presTimeSecs_high_annulus_11= high_init;
presTimeSecs_high_annulus_21= high_init;
presTimeSecs_high_annulus_12= high_init;
presTimeSecs_high_annulus_22= high_init;

stepSize_low_center_1 = initial_stepSize;
stepSize_low_center_2= initial_stepSize;
stepSize_low_patch_1 = initial_stepSize;
stepSize_low_patch_2 = initial_stepSize;
stepSize_low_annulus_11 = initial_stepSize;
stepSize_low_annulus_21 = initial_stepSize;
stepSize_low_annulus_12 = initial_stepSize;
stepSize_low_annulus_22 = initial_stepSize;

stepSize_high_center_1 = initial_stepSize;
stepSize_high_center_2= initial_stepSize;
stepSize_high_patch_1 = initial_stepSize;
stepSize_high_patch_2 = initial_stepSize;
stepSize_high_annulus_11 = initial_stepSize;
stepSize_high_annulus_21 = initial_stepSize;
stepSize_high_annulus_12 = initial_stepSize;
stepSize_high_annulus_22 = initial_stepSize;

% Interstimulus interval time in seconds and frames
isiTimeSecs = 1;
isiTimeFrames = round(isiTimeSecs / ifi);

% Numer of frames to wait before re-drawing
waitframes = 1;

% Gabor information

```

```

% Count how many Gabors there are
nGabors = 1;

% Drift speed for the 2D global motion
degPerSec = 360 * 2;
degPerFrame = degPerSec * ifi;

gaborAngles = pi/2;
degPerFrameGabors = cosd(gaborAngles) .* degPerFrame;

% Randomise the phase of the Gabors and make a ...
% properties matrix.
phaseLine = rand(1, nGabors) .* 360;

% Experimental loop

correctInaRowlow_center_1= 0;
correctInaRowlow_center_2= 0;
correctInaRowlow_patch_1= 0;
correctInaRowlow_patch_2= 0;
correctInaRowlow_annulus_11= 0;
correctInaRowlow_annulus_21= 0;
correctInaRowlow_annulus_12= 0;
correctInaRowlow_annulus_22= 0;

correctInaRowhigh_center_1= 0;
correctInaRowhigh_center_2= 0;
correctInaRowhigh_patch_1= 0;
correctInaRowhigh_patch_2= 0;
correctInaRowhigh_annulus_11= 0;
correctInaRowhigh_annulus_21= 0;
correctInaRowhigh_annulus_12= 0;
correctInaRowhigh_annulus_22= 0;

```

```
counter_low_center_1= 0;  
counter_low_center_2= 0;  
counter_low_patch_1= 0;  
counter_low_patch_2= 0;  
counter_low_annulus_11= 0;  
counter_low_annulus_21= 0;  
counter_low_annulus_12= 0;  
counter_low_annulus_22= 0;
```

```
counter_high_center_1= 0;  
counter_high_center_2= 0;  
counter_high_patch_1= 0;  
counter_high_patch_2= 0;  
counter_high_annulus_11= 0;  
counter_high_annulus_21= 0;  
counter_high_annulus_12= 0;  
counter_high_annulus_22= 0;
```

```
accuracy_low_center_1= zeros(1,numTrials);  
accuracy_low_center_2= zeros(1,numTrials);  
accuracy_low_patch_1= zeros(1,numTrials);  
accuracy_low_patch_2= zeros(1,numTrials);  
accuracy_low_annulus_11= zeros(1,numTrials);  
accuracy_low_annulus_21= zeros(1,numTrials);  
accuracy_low_annulus_12= zeros(1,numTrials);  
accuracy_low_annulus_22= zeros(1,numTrials);
```

```
accuracy_high_center_1= zeros(1,numTrials);  
accuracy_high_center_2= zeros(1,numTrials);  
accuracy_high_patch_1= zeros(1,numTrials);  
accuracy_high_patch_2= zeros(1,numTrials);  
accuracy_high_annulus_11= zeros(1,numTrials);
```

```

accuracy_high_annulus_21= zeros(1,numTrials);
accuracy_high_annulus_12= zeros(1,numTrials);
accuracy_high_annulus_22= zeros(1,numTrials);

reversal_low_center_1=0; reversal_low_center_2=0;
reversal_low_patch_1=0; reversal_low_patch_2=0;
reversal_low_annulus_11=0; reversal_low_annulus_21=0;
reversal_low_annulus_12=0; reversal_low_annulus_22=0;

reversal_high_center_1=0; reversal_high_center_2=0;
reversal_high_patch_1=0; reversal_high_patch_2=0;
reversal_high_annulus_11=0; reversal_high_annulus_21=0;
reversal_high_annulus_12=0; reversal_high_annulus_22=0;

% Animation loop: we loop for the total number of trials
for trial = 1:numTrials

    theDriftdirection = DriftdirectionList(trial);
    thePatchSize = condMatrixShuffled(1, trial);
    theCenterSize = condMatrixShuffled(2, trial);
    theCond = condMatrixShuffled(3, trial);

    if theCenterSize == centerSizeList(1)
        centerDeg=centerDegList(1);
    elseif theCenterSize == centerSizeList(2)
        centerDeg=centerDegList(2);
    end

    if thePatchSize == patchSizeList(1)
        patchDeg=patchDegList(1);
    elseif thePatchSize == patchSizeList(2)
        patchDeg=patchDegList(2);

```

end

% Spatial Frequency (Cycles Per Pixel)

numCycles_center = centerDeg*2;

numCycles_patch = patchDeg*2;

freq1 = numCycles_center / theCenterSize;

freq2 = numCycles_patch / thePatchSize;

% Build a procedural gabor texture

if theCond == 1

gabortex_center = ...

CreateProceduralSmoothedApertureSineGrating...

(window, theCenterSize, theCenterSize, ...

[grey grey grey 0.0],...

theCenterSize/2, 1, 25, [], []);

else

gabortex_center = ...

CreateProceduralSmoothedApertureSineGrating...

(window, theCenterSize, theCenterSize, ...

[grey grey grey 0.0],...

theCenterSize/2, 1, thePatchSize/2, [], []);

gabortex_patch = ...

CreateProceduralSmoothedApertureSineGrating...

(window, thePatchSize, thePatchSize, ...

[grey grey grey 0.0],...

thePatchSize/2, 1, thePatchSize/2, [], []);

end

% radius of the disc edge

radius = theCenterSize / 2;

% smoothing sigma in pixel

sigma = theCenterSize / 6;

% use alpha channel for smoothing edge of disc?

```

useAlpha = true;
% smoothing method: cosine (0), smoothstep (1), ...
% inverse smoothstep (2)
smoothMethod = 0;

% Build a procedural disc
disctexture = CreateProceduralSmoothedDisc(window, ...
theCenterSize, theCenterSize, [0 0 0 0], radius, ...
sigma, useAlpha, smoothMethod);

% Cue to determine whether a response has been made
respToBeMade = true;
Screen('BlendFunction', window, 'GL_SRC_ALPHA', ...
'GL_ONE_MINUS_SRC_ALPHA');

% If this is the first trial we present a start screen
and wait for a key-press
if trial == 1
    DrawFormattedText(window, 'Press Any Key ...
    To Begin', 'center', 'center', black);
    Screen('Flip', window);
    KbStrokeWait;
elseif trial == 289
    DrawFormattedText(window, 'Rest Your Eyes. ...
    1/5 is complete.', 'center', 'center', black);
    Screen('Flip', window);
    KbStrokeWait;
elseif trial == 578
    DrawFormattedText(window, 'Rest Your Eyes. ...
    2/5 is complete.', 'center', 'center', black);
    Screen('Flip', window);
    KbStrokeWait;
elseif trial == 866

```

```

        DrawFormattedText(window, 'Rest Your Eyes. ...
        3/5 is complete.', 'center', 'center', black);
        Screen('Flip', window);
        KbStrokeWait;
elseif trial == 1154
        DrawFormattedText(window, 'Rest Your Eyes. ...
        4/5 is complete.', 'center', 'center', black);
        Screen('Flip', window);
        KbStrokeWait;
end

% Flip again to sync us to the vertical retrace
at the same time as drawing our fixation point
Screen('DrawDots', window, [xCenter; yCenter], ...
1, black, [], 2);
vbl = Screen('Flip', window);

for frame = 1:isiTimeFrames - 1

        % Draw the fixation point
        Screen('DrawDots', window, [xCenter; yCenter], ...
        1, black, [], 2);

        % Flip to the screen
        vbl = Screen('Flip', window, vbl + (waitframes...
        - 0.5) * ifi);
end

% Presentation Time for the Gabor in seconds ...
% and frames
if stair_cond(trial) == 1

        if (theCond == 1) && (theCenterSize ==...

```

```

centerSizeList(1))
    presTimeSecs = presTimeSecs_low_center_1;
elseif (theCond == 1) && (theCenterSize == ...
centerSizeList(2))
    presTimeSecs = presTimeSecs_low_center_2;
elseif (theCond == 3) && (thePatchSize == ...
patchSizeList(1))
    presTimeSecs = presTimeSecs_low_patch_1;
elseif (theCond == 3) && (thePatchSize == ...
patchSizeList(2))
    presTimeSecs = presTimeSecs_low_patch_2;
elseif (theCond == 2) && (theCenterSize == ...
centerSizeList(1)) && (thePatchSize == ...
patchSizeList(1))
    presTimeSecs = presTimeSecs_low_annulus_11;
elseif (theCond == 2) && (theCenterSize == ...
centerSizeList(1)) && (thePatchSize == ...
patchSizeList(2))
    presTimeSecs = presTimeSecs_low_annulus_12;
elseif (theCond == 2) && (theCenterSize == ...
centerSizeList(2)) && (thePatchSize == ...
patchSizeList(1))
    presTimeSecs = presTimeSecs_low_annulus_21;
elseif (theCond == 2) && (theCenterSize == ...
centerSizeList(2)) && (thePatchSize == ...
patchSizeList(2))
    presTimeSecs = presTimeSecs_low_annulus_22;
end

```

```

elseif stair_cond(trial) == 2

```

```

    if (theCond == 1) && (theCenterSize == ...
centerSizeList(1))

```

```

        presTimeSecs = presTimeSecs_high_center_1;
    elseif (theCond == 1) && (theCenterSize == ...
        centerSizeList(2))
        presTimeSecs = presTimeSecs_high_center_2;
    elseif (theCond == 3) && (thePatchSize == ...
        patchSizeList(1))
        presTimeSecs = presTimeSecs_high_patch_1;
    elseif (theCond == 3) && (thePatchSize == ...
        patchSizeList(2))
        presTimeSecs = presTimeSecs_high_patch_2;
    elseif (theCond == 2) && (theCenterSize == ...
        centerSizeList(1)) && (thePatchSize == ...
        patchSizeList(1))
        presTimeSecs = presTimeSecs_high_annulus_11;
    elseif (theCond == 2) && (theCenterSize == ...
        centerSizeList(1)) && (thePatchSize == ...
        patchSizeList(2))
        presTimeSecs = presTimeSecs_high_annulus_12;
    elseif (theCond == 2) && (theCenterSize == ...
        centerSizeList(2)) && (thePatchSize == ...
        patchSizeList(1))
        presTimeSecs = presTimeSecs_high_annulus_21;
    elseif (theCond == 2) && (theCenterSize == ...
        centerSizeList(2)) && (thePatchSize == ...
        patchSizeList(2))
        presTimeSecs = presTimeSecs_high_annulus_22;
end

```

end

```

presTimeFrames = round(presTimeSecs / ifi);
% Now we draw the Gabor and the fixation point
tic

```

```

for frame = 1:presTimeFrames

    %Temporal ramp
    d= presTimeFrames*0.25; %0.56
    s= (median(1:presTimeFrames));
    gauss=exp(-((frame-2*(s/2))^2)/(2*(d^2)));
    theContrast=Contrast*gauss;

    propertiesMatCenter = repmat([NaN, freq1, ...
    theContrast, 0], nGabors ,1);
    propertiesMatCenter(:, 1) = phaseLine';
    propertiesMat1 = propertiesMatCenter;
    propertiesMatPatch = repmat([NaN, freq2, ...
    theContrast, 0], nGabors ,1);
    propertiesMatPatch(:, 1) = phaseLine';
    propertiesMat2 = propertiesMatPatch;

    Screen('BlendFunction', window, 'GLONE', ...
    'GLZERO');

    if theCond == 1
        Screen('DrawTextures', window, ...
        gabortex_center, [], [], gaborAngles, ...
        [], [], [grey grey grey], [], [], ...
        propertiesMat1 ');

    elseif theCond == 2
        Screen('DrawTextures', window, ...
        gabortex_patch, [], [], gaborAngles, ...
        [], [], [grey grey grey], [], [], ...
        propertiesMat2 ');
        Screen('BlendFunction', window, ...

```

```

        'GL_SRC_ALPHA', 'GL_ONE_MINUS_SRC_ALPHA');
Screen('DrawTextures', window, ...
    discTexture, [], [], [], [], [], ...
    [grey grey grey], [], [], []);
Screen('BlendFunction', window, ...
    'GL_ONE', 'GL_ZERO');

elseif theCond == 3
    Screen('DrawTextures', window, ...
        gaborTex_patch, [], [], gaborAngles, ...
        [], [], [grey grey grey], [], [], ...
        propertiesMat2');
end

Screen('BlendFunction', window, 'GL_SRC_ALPHA', ...
    'GL_ONE_MINUS_SRC_ALPHA');

% Draw the fixation point
Screen('DrawDots', window, [xCenter; yCenter], ...
    1, black, [], 2);
% Flip to the screen
vbl = Screen('Flip', window, vbl + (waitframes ...
    - 0.5) * ifi);

% Increment the phase of our Gabors
phaseLine = phaseLine + (theDriftDirection * ...
    degPerFrameGabors);
end

elapsedTime = toc;
% Change the blend function to draw an ...
% antialiased fixation point
Screen('BlendFunction', window, 'GL_SRC_ALPHA', ...

```

```

'GL_ONE_MINUS_SRC_ALPHA');

% Draw the fixation point
Screen('DrawDots', window, [xCenter; yCenter], ...
1, black, [], 2);

% Flip to the screen
vbl = Screen('Flip', window, vbl + (waitframes ...
- 0.5) * ifi);

%Now I start the response detection loop
tStart = vbl;
accuracy=0;
while respToBeMade == true

    % Check the keyboard. The person should press the
    [keyIsDown, secs, keyCode] = KbCheck;
    if keyCode(escapeKey)
        ShowCursor;
        sca;
        return
    elseif (keyCode(leftKey) && ...
theDriftdirection == 1)...
    || (keyCode(rightKey) && theDriftdirection == -1)
        accuracy=1; %correct answer
        respToBeMade = false;
    elseif (keyCode(leftKey) && ...
theDriftdirection == -1) ...
    || (keyCode(rightKey) && theDriftdirection == 1)
        accuracy=0; %incorrect answer
        respToBeMade = false;
    elseif keyIsDown
        badkey=true;

```

```

    end
end
% calculate the dependent variables (RTs and accuracy)
tEnd = GetSecs;
RT = tEnd - tStart;

fprintf(fp, '%15d\t%15d\t%15d\t%15d\t%15d\t%15.2f\t ...
%15d\t%15.3f\t%15.4f\t%15.4f\n', trial, ...
theCenterSize, thePatchSize, theCond, ...
stair_cond(trial), theContrast, ...
accuracy, RT, presTimeSecs, elapsedTime);

if (stair_cond(trial)==1) && (accuracy==1)

    if (theCond == 1) && (theCenterSize == ...
centerSizeList(1))
        correctInaRowlow_center_1 = ...
        correctInaRowlow_center_1 + 1;
        counter_low_center_1= counter_low_center_1 ...
        + 1;
        accuracy_low_center_1(counter_low_center_1)...
        = 1;

    elseif (theCond == 1) && (theCenterSize == ...
centerSizeList(2))
        correctInaRowlow_center_2 = ...
        correctInaRowlow_center_2 +1;
        counter_low_center_2= counter_low_center_2 ...
        + 1;
        accuracy_low_center_2(counter_low_center_2)...
        = 1;

    elseif(theCond == 3) && (thePatchSize == ...

```

```

patchSizeList(1))
    correctInaRowlow_patch_1 = ...
    correctInaRowlow_patch_1 +1;
    counter_low_patch_1 = counter_low_patch_1 ...
    + 1;
    accuracy_low_patch_1(counter_low_patch_1)...
    = 1;

elseif(theCond == 3) && (thePatchSize == ...
patchSizeList(2))
    correctInaRowlow_patch_2 = ...
    correctInaRowlow_patch_2 +1;
    counter_low_patch_2 = counter_low_patch_2 ...
    + 1;
    accuracy_low_patch_2(counter_low_patch_2)...
    = 1;

elseif (theCond == 2) && (theCenterSize == ...
centerSizeList(1)) && (thePatchSize == ...
patchSizeList(1))
    correctInaRowlow_annulus_11 = ...
    correctInaRowlow_annulus_11 +1;
    counter_low_annulus_11 = ...
    counter_low_annulus_11 + 1;
    accuracy_low_annulus_11 ...
    (counter_low_annulus_11)=1;

elseif (theCond == 2) && (theCenterSize == ...
centerSizeList(1)) && (thePatchSize == ...
patchSizeList(2))
    correctInaRowlow_annulus_12 = ...
    correctInaRowlow_annulus_12 +1;
    counter_low_annulus_12 = ...

```

```

        counter_low_annulus_12 + 1;
        accuracy_low_annulus_12 ...
        (counter_low_annulus_12)=1;

elseif (theCond == 2) && (theCenterSize == ...
centerSizeList(2)) && (thePatchSize == ...
patchSizeList(1))
    correctInaRowlow_annulus_21 = ...
    correctInaRowlow_annulus_21 +1;
    counter_low_annulus_21 = ...
    counter_low_annulus_21 + 1;
    accuracy_low_annulus_21 ...
    (counter_low_annulus_21)=1;

elseif (theCond == 2) && (theCenterSize == ...
centerSizeList(2)) && (thePatchSize == ...
patchSizeList(2))
    correctInaRowlow_annulus_22 = ...
    correctInaRowlow_annulus_22 +1;
    counter_low_annulus_22 = ...
    counter_low_annulus_22 + 1;
    accuracy_low_annulus_22 ...
    (counter_low_annulus_22)=1;

end

if correctInaRowlow_center_1 == 3
    [reversal_low_center_1 , ...
    stepSize_low_center_1 , ...
    presTimeSecs_low_center_1 , ...
    correctInaRowlow_center_1] = ...
    stair1(accuracy_low_center_1 , ...
        counter_low_center_1 , ...

```

```

        reversal_low_center_1 , ...
        stepSize_low_center_1 , ...
        presTimeSecs_low_center_1 );

elseif correctInaRowlow_center_2 == 3
    [reversal_low_center_2 , ...
    stepSize_low_center_2 ...
    ,presTimeSecs_low_center_2 , ...
    correctInaRowlow_center_2] = ...
    stair1 (accuracy_low_center_2 , ...
            counter_low_center_2 , ...
            reversal_low_center_2 ...
            ,stepSize_low_center_2 , ...
            presTimeSecs_low_center_2 );

elseif correctInaRowlow_patch_1 == 3
    [reversal_low_patch_1 , ...
    stepSize_low_patch_1 , ...
    presTimeSecs_low_patch_1 , ...
    correctInaRowlow_patch_1] = ...
    stair1 (accuracy_low_patch_1 , ...
            counter_low_patch_1 , ...
            reversal_low_patch_1 , ...
            stepSize_low_patch_1 , ...
            presTimeSecs_low_patch_1 );

elseif correctInaRowlow_patch_2 == 3
    [reversal_low_patch_2 , stepSize_low_patch_2 ...
    ,presTimeSecs_low_patch_2 , ...
    correctInaRowlow_patch_2] = ...
    stair1 (accuracy_low_patch_2 , ...
            counter_low_patch_2 , ...
            reversal_low_patch_2 , ...

```

```

        stepSize_low_patch_2 , ...
        presTimeSecs_low_patch_2 );

elseif correctInaRowlow_annulus_11 == 3
    [reversal_low_annulus_11 , ...
    stepSize_low_annulus_11 , ...
    presTimeSecs_low_annulus_11 , ...
    correctInaRowlow_annulus_11] = ...
    stair1 (accuracy_low_annulus_11 , ...
            counter_low_annulus_11 , ...
            reversal_low_annulus_11 , ...
            stepSize_low_annulus_11 , ...
            presTimeSecs_low_annulus_11 );

elseif correctInaRowlow_annulus_12 == 3
    [reversal_low_annulus_12 , ...
    stepSize_low_annulus_12 , ...
    presTimeSecs_low_annulus_12 , ...
    correctInaRowlow_annulus_12] = ...
    stair1 (accuracy_low_annulus_12 , ...
            counter_low_annulus_12 , ...
            reversal_low_annulus_12 , ...
            stepSize_low_annulus_12 , ...
            presTimeSecs_low_annulus_12 );

elseif correctInaRowlow_annulus_21 == 3
    [reversal_low_annulus_21 , ...
    stepSize_low_annulus_21 , ...
    presTimeSecs_low_annulus_21 , ...
    correctInaRowlow_annulus_21] = stair1 ...
    (accuracy_low_annulus_21 , ...
     counter_low_annulus_21 , ...
     reversal_low_annulus_21 ...

```

```

        ,stepSize_low_annulus_21 , ...
        presTimeSecs_low_annulus_21);

elseif correctInaRowlow_annulus_22 == 3
    [reversal_low_annulus_22 , ...
    stepSize_low_annulus_22 , ...
    presTimeSecs_low_annulus_22 ,...
    correctInaRowlow_annulus_22] = ...
    stair1(accuracy_low_annulus_22 , ...
           counter_low_annulus_22 , ...
           reversal_low_annulus_22 ...
           ,stepSize_low_annulus_22 , ...
           presTimeSecs_low_annulus_22);
end

elseif (stair_cond(trial)==1) && (accuracy==0)

if (theCond== 1) && (theCenterSize == ...
centerSizeList(1))
    [reversal_low_center_1 ,stepSize_low_center_1 ,
    presTimeSecs_low_center_1 , ...
    correctInaRowlow_center_1 , ...
    counter_low_center_1] = stair0(...
    accuracy_low_center_1 , ...
    counter_low_center_1 , ...
    reversal_low_center_1 , ...
    stepSize_low_center_1 , ...
    presTimeSecs_low_center_1);

elseif (theCond== 1) && (theCenterSize == ...
centerSizeList(2))
    [reversal_low_center_2 , ...
    stepSize_low_center_2 , ...

```

```

presTimeSecs_low_center_2 , ...
correctInaRow_low_center_2 , counter_low_center_2] = stair0 (a
    counter_low_center_2 , ...
    reversal_low_center_2 , ...
    stepSize_low_center_2 , ...
    presTimeSecs_low_center_2);

elseif (theCond== 3) && (thePatchSize == ...
patchSizeList(1))
    [reversal_low_patch_1 , ...
    stepSize_low_patch_1 , ...
    presTimeSecs_low_patch_1 , ...
    correctInaRow_low_patch_1 , ...
    counter_low_patch_1]=stair0 (...
    accuracy_low_patch_1 , ...
        counter_low_patch_1 , ...
        reversal_low_patch_1 , ...
        stepSize_low_patch_1 , ...
        presTimeSecs_low_patch_1);

elseif (theCond== 3) && (thePatchSize == ...
patchSizeList(2))
    [reversal_low_patch_2 , ...
    stepSize_low_patch_2 , ...
    presTimeSecs_low_patch_2 , ...
    correctInaRow_low_patch_2 , ...
    counter_low_patch_2]=stair0 (...
    accuracy_low_patch_2 ,...
        counter_low_patch_2 , ...
        reversal_low_patch_2 , ...
        stepSize_low_patch_2 , ...
        presTimeSecs_low_patch_2);

```

```

elseif (theCond== 2) && (theCenterSize == ...
centerSizeList(1)) && (thePatchSize == ...
patchSizeList(1))
    [reversal_low_annulus_11 , ...
    stepSize_low_annulus_11 , ...
    presTimeSecs_low_annulus_11 , ...
    correctInaRow_low_annulus_11 , ...
    counter_low_annulus_11]=stair0 (...
    accuracy_low_annulus_11 ,...
        counter_low_annulus_11 , ...
        reversal_low_annulus_11 , ...
        stepSize_low_annulus_11 , ...
        presTimeSecs_low_annulus_11);

elseif (theCond== 2) && (theCenterSize == ...
centerSizeList(1)) && (thePatchSize == ...
patchSizeList(2))
    [reversal_low_annulus_12 , ...
    stepSize_low_annulus_12 , ...
    presTimeSecs_low_annulus_12 , ...
    correctInaRow_low_annulus_12 , ...
    counter_low_annulus_12]=stair0 (...
    accuracy_low_annulus_12 ,...
        counter_low_annulus_12 , ...
        reversal_low_annulus_12 , ...
        stepSize_low_annulus_12 ,...
        presTimeSecs_low_annulus_12);

elseif (theCond== 2) && (theCenterSize == ...
centerSizeList(2)) && (thePatchSize == ...
patchSizeList(1))
    [reversal_low_annulus_21 , ...
    stepSize_low_annulus_21 , ...

```

```

presTimeSecs_low_annulus_21 , ...
correctInaRow_low_annulus_21 , ...
counter_low_annulus_21]=stair0 (...
accuracy_low_annulus_21 ,...
    counter_low_annulus_21 , ...
    reversal_low_annulus_21 , ...
    stepSize_low_annulus_21 , ...
    presTimeSecs_low_annulus_21 );

elseif (theCond== 2) && (theCenterSize == ...
centerSizeList(2)) && (thePatchSize == ...
patchSizeList(2))
    [reversal_low_annulus_22 , ...
    stepSize_low_annulus_22 , ...
    presTimeSecs_low_annulus_22 , ...
    correctInaRow_low_annulus_22 , ...
    counter_low_annulus_22]=stair0 (...
    accuracy_low_annulus_22 ,...
        counter_low_annulus_22 , ...
        reversal_low_annulus_22 , ...
        stepSize_low_annulus_22 , ...
        presTimeSecs_low_annulus_22 );

end

elseif (stair_cond(trial)==2) && (accuracy==1)

    if (theCond == 1) && (theCenterSize == ...
centerSizeList(1))
        correctInaRow_high_center_1 = ...
        correctInaRow_high_center_1 +1;
        counter_high_center_1 = ...
        counter_high_center_1 + 1;
        accuracy_high_center_1 (...

```

```

        counter_high_center_1) = 1;

elseif (theCond == 1) && (theCenterSize == ...
centerSizeList(2))
    correctInaRowhigh_center_2 = ...
    correctInaRowhigh_center_2 +1;
    counter_high_center_2 = ...
    counter_high_center_2 + 1;
    accuracy_high_center_2(...
    counter_high_center_2)=1;

elseif(theCond == 3) && (thePatchSize == ...
patchSizeList(1))
    correctInaRowhigh_patch_1 = ...
    correctInaRowhigh_patch_1 +1;
    counter_high_patch_1 = ...
    counter_high_patch_1 + 1;
    accuracy_high_patch_1(...
    counter_high_patch_1)=1;

elseif(theCond == 3) && (thePatchSize == ...
patchSizeList(2))
    correctInaRowhigh_patch_2 = ...
    correctInaRowhigh_patch_2 +1;
    counter_high_patch_2 = ...
    counter_high_patch_2 + 1;
    accuracy_high_patch_2(...
    counter_high_patch_2)=1;

elseif (theCond == 2) && (theCenterSize == ...
centerSizeList(1)) && (thePatchSize == ...
patchSizeList(1))
    correctInaRowhigh_annulus_11 = ...

```

```

        correctInaRowhigh-annulus_11 +1;
        counter_high-annulus_11= ...
        counter_high-annulus_11 + 1;
        accuracy_high-annulus_11 (...
        counter_high-annulus_11)=1;

elseif (theCond == 2) && (theCenterSize == ...
centerSizeList(1)) && (thePatchSize ==...
patchSizeList(2))
        correctInaRowhigh-annulus_12 = ...
        correctInaRowhigh-annulus_12 + 1;
        counter_high-annulus_12 = ...
        counter_high-annulus_12 + 1;
        accuracy_high-annulus_12 (...
        counter_high-annulus_12)=1;

elseif (theCond == 2) && (theCenterSize == ...
centerSizeList(2)) && (thePatchSize == ...
patchSizeList(1))
        correctInaRowhigh-annulus_21 = ...
        correctInaRowhigh-annulus_21 +1;
        counter_high-annulus_21 = ...
        counter_high-annulus_21 + 1;
        accuracy_high-annulus_21 (...
        counter_high-annulus_21)=1;

elseif (theCond == 2) && (theCenterSize == ...
centerSizeList(2)) && (thePatchSize == ...
patchSizeList(2))
        correctInaRowhigh-annulus_22 = ...
        correctInaRowhigh-annulus_22 +1;
        counter_high-annulus_22 = ...
        counter_high-annulus_22 + 1;

```

```

        accuracy_high_annulus_22 (...
        counter_high_annulus_22)=1;

end

if correctInaRowhigh_center_1 == 3
    [reversal_high_center_1 ,...
    stepSize_high_center_1 , ...
    presTimeSecs_high_center_1 , ...
    correctInaRowhigh_center_1]= ...
    stair1 (accuracy_high_center_1 ,...
            counter_high_center_1 ,...
            reversal_high_center_1 ...
            ,stepSize_high_center_1 , ...
            presTimeSecs_high_center_1 );

elseif correctInaRowhigh_center_2 == 3
    [reversal_high_center_2 , ...
    stepSize_high_center_2 , ...
    presTimeSecs_high_center_2 , ...
    correctInaRowhigh_center_2]= ...
    stair1 (accuracy_high_center_2 , ...
            counter_high_center_2 , ...
            reversal_high_center_2 , ...
            stepSize_high_center_2 , ...
            presTimeSecs_high_center_2 );

elseif correctInaRowhigh_patch_1 == 3
    [reversal_high_patch_1 , ...
    stepSize_high_patch_1 ...
    ,presTimeSecs_high_patch_1 , ...
    correctInaRowhigh_patch_1]= ...
    stair1 (accuracy_high_patch_1 ,

```

```

        counter_high_patch_1 , ...
        reversal_high_patch_1 , ...
        stepSize_high_patch_1 , ...
        presTimeSecs_high_patch_1 );

elseif correctInaRowhigh_patch_2 == 3
    [reversal_high_patch_2 , ...
    stepSize_high_patch_2 ...
    ,presTimeSecs_high_patch_2 , ...
    correctInaRowhigh_patch_2]= ...
    stair1(accuracy_high_patch_2 , ...
        counter_high_patch_2 , ...
        reversal_high_patch_2 , ...
        stepSize_high_patch_2 , ...
        presTimeSecs_high_patch_2);

elseif correctInaRowhigh_annulus_11 == 3
    [reversal_high_annulus_11 , ...
    stepSize_high_annulus_11 , ...
    presTimeSecs_high_annulus_11 , ...
    correctInaRowhigh_annulus_11 ]...
    = stair1(accuracy_high_annulus_11 , ...
        counter_high_annulus_11 , ...
        reversal_high_annulus_11 ...
        ,stepSize_high_annulus_11 , ...
        presTimeSecs_high_annulus_11);

elseif correctInaRowhigh_annulus_21 == 3
    [reversal_high_annulus_21 , ...
    stepSize_high_annulus_21 , ...
    ,presTimeSecs_high_annulus_21 , ...
    correctInaRowhigh_annulus_21 ]...
    = stair1(accuracy_high_annulus_21 , ...

```

```

        counter_high-annulus_21 , ...
        reversal_high-annulus_21 ...
        ,stepSize_high-annulus_21 , ...
        presTimeSecs_high-annulus_21 );

elseif correctInaRowhigh-annulus_12 == 3
    [reversal_high-annulus_12 , ...
    stepSize_high-annulus_12 ...
    ,presTimeSecs_high-annulus_12 , ...
    correctInaRowhigh-annulus_12 ]...
    = stair1(accuracy_high-annulus_12 ,...
        counter_high-annulus_12 , ...
        reversal_high-annulus_12 , ...
        stepSize_high-annulus_12 , ...
        presTimeSecs_high-annulus_12 );

elseif correctInaRowhigh-annulus_22 == 3
    [reversal_high-annulus_22 , ...
    stepSize_high-annulus_22 , ...
    presTimeSecs_high-annulus_22 , ...
    correctInaRowhigh-annulus_22 ]...
    = stair1(accuracy_high-annulus_22 ,...
        counter_high-annulus_22 , ...
        reversal_high-annulus_22 , ...
        stepSize_high-annulus_22 , ...
        presTimeSecs_high-annulus_22 );

end

elseif (stair_cond(trial)==2) && (accuracy==0)

    if (theCond== 1) && (theCenterSize == ...
    centerSizeList(1))

```

```

[reversal_high_center_1 , ...
stepSize_high_center_1 ...
, presTimeSecs_high_center_1 , ...
correctInaRow_high_center_1 , ...
counter_high_center_1] = stair0 (...
accuracy_high_center_1 , ...
    counter_high_center_1 , ...
    reversal_high_center_1 , ...
    stepSize_high_center_1 , ...
    presTimeSecs_high_center_1);

elseif (theCond== 1) && (theCenterSize == ...
centerSizeList(2))
    [reversal_high_center_2 , ...
stepSize_high_center_2 , ...
presTimeSecs_high_center_2 , ...
correctInaRow_high_center_2 , ...
counter_high_center_2]=stair0 (...
accuracy_high_center_2 ,...
    counter_high_center_2 , ...
    reversal_high_center_2 , ...
    stepSize_high_center_2 , ...
    presTimeSecs_high_center_2);

elseif (theCond== 3) && (thePatchSize == ...
patchSizeList(1))
    [reversal_high_patch_1 , ...
stepSize_high_patch_1 , ...
presTimeSecs_high_patch_1 , ...
correctInaRow_high_patch_1 , ...
counter_high_patch_1]=stair0 (...
accuracy_high_patch_1 ,...
    counter_high_patch_1 , ...

```

```

        reversal_high_patch_1 ...
        , stepSize_high_patch_1 , ...
        presTimeSecs_high_patch_1 );

elseif (theCond== 3) && (thePatchSize == ...
patchSizeList(2))
    [reversal_high_patch_2 , ...
    stepSize_high_patch_2 ...
    , presTimeSecs_high_patch_2 , ...
    correctInaRow_high_patch_2 , ...
    counter_high_patch_2]=stair0 (...
    accuracy_high_patch_2 ,...
        counter_high_patch_2 , ...
        reversal_high_patch_2 , ...
        stepSize_high_patch_2 , ...
        presTimeSecs_high_patch_2 );

elseif (theCond== 2) && (theCenterSize == ...
centerSizeList(1)) && (thePatchSize == ...
patchSizeList(1))
    [reversal_high_annulus_11 , ...
    stepSize_high_annulus_11 , ...
    presTimeSecs_high_annulus_11 , ...
    correctInaRow_high_annulus_11 ,...
    counter_high_annulus_11]=stair0 (...
    accuracy_high_annulus_11 ,...
        counter_high_annulus_11 , ...
        reversal_high_annulus_11 , ...
        stepSize_high_annulus_11 , ...
        presTimeSecs_high_annulus_11 );

elseif (theCond== 2) && (theCenterSize == ...
centerSizeList(1)) && (thePatchSize == ...

```

```

patchSizeList(2))
    [reversal_high_annulus_12, ...
    stepSize_high_annulus_12, ...
    presTimeSecs_high_annulus_12, ...
    correctInaRow_high_annulus_12, ...
    counter_high_annulus_12]=stair0(...
    accuracy_high_annulus_12, ...
        counter_high_annulus_12, ...
        reversal_high_annulus_12, ...
        stepSize_high_annulus_12, ...
        presTimeSecs_high_annulus_12);

elseif (theCond== 2) && (theCenterSize == ...
centerSizeList(2)) && (thePatchSize == ...
patchSizeList(1))
    [reversal_high_annulus_21, ...
    stepSize_high_annulus_21, ...
    presTimeSecs_high_annulus_21, ...
    correctInaRow_high_annulus_21, ...
    counter_high_annulus_21]=stair0(...
    accuracy_high_annulus_21, ...
        counter_high_annulus_21, ...
        reversal_high_annulus_21, ...
        stepSize_high_annulus_21, ...
        presTimeSecs_high_annulus_21);

elseif (theCond== 2) && (theCenterSize == ...
centerSizeList(2)) && (thePatchSize == ...
patchSizeList(2))
    [reversal_high_annulus_22, ...
    stepSize_high_annulus_22, ...
    presTimeSecs_high_annulus_22, ...
    correctInaRow_high_annulus_22, ...

```

```

        counter_high_annulus_22]=stair0 (...
        accuracy_high_annulus_22 ,...
            counter_high_annulus_22 , ...
            reversal_high_annulus_22 ...
            ,stepSize_high_annulus_22 , ...
            presTimeSecs_high_annulus_22 );

    end

end

end

DrawFormattedText(window, 'Experiment_Finished_\n\n...
Press_Any_Key_To_Exit ', 'center', 'center', black);
Screen('Flip', window);
KbStrokeWait;
sca;
fclose(fp);
close all;

```

Listing B.2: Divisive normalization model

```

function model
% Usage: simply call the function to produce model
% figures, or walk through each cell
%
% Inputs: none
% Outputs: none
%
% Authors: Scott O. Murray, Michael-Paul Schallmo
% University of Washington, Dept. of Psychology
% c. July 2017
% This code implements the "basic" normalization model to

```

```

% describe spatial suppression and summation during ...
% a motion direction discrimination paradigm, as ...
% detailed in Schallmo, M-P., Kale, A.M., Millin, R., ...
% Flevaris, A.V., Brkanac, Z., Edden, R.A.E., ...
% Bernier, R.A., Murray, S.O. (2017). ‘‘Suppression and
% facilitation of human neural responses ‘‘
% Available at: https:
% //www.biorxiv.org/content/early/2017/08/10/174466
%
% Uses code by Geoff M. Boynton
% University of Washington, Dept. of Psychology
% – Specifically: makeNeuralImage.m & convolveImage.m
% – These will need to be in your path to run the
% code below.
%
% Adapted from code by Reynolds & Heeger (2009), ...
% from their paper entitled ‘‘The Normalization Model ...
% of Attention ‘‘ in Neuron, 61(2), p. 168–185
% Their original code is available from:
% http://www.snl-r.salk.edu/~reynolds/
% Normalization_Model_of_Attention/
% http://www.cns.nyu.edu/heegerlab/?page=software

%% set up model parameters
% list of stimulus positions (arbitrary coordinates)
p.x = -600:2:600;
% list of orientations (degrees)
p.theta = -600:2:600;

area = 'MT'
switch area
    case 'V1'
        p.e.x.width = 2; %V1 excitation spatial width

```

```

p.e.theta.width = 5; %V1 excitation orientation width
p.i.x.width = 8; %V1 suppression spatial width
p.i.theta.width = 10; %V1 excitation orientation width
stim.theta.width = 5; %V1 stimulus orientation width
Criterion = [20000 23000];

case 'MT'
    p.e.x.width = 5; %MT excitation spatial width
    p.e.theta.width = 20; %MT excitation orientation width
    p.i.x.width = 20; %MT suppression spatial width
    p.i.theta.width = 50; %MT excitation orientation width
    stim.theta.width = 5; %MT stimulus orientation width
    Criterion = [80000 100000];
end

p.sigma = .0002; %semi-saturation constant
stim.theta.center = 0; %stimulus orientation
stim.x.center = 0; %stimulus position

%% generate model pieces
xWidth = 1:.5:12;
%range of stimulus contrasts to examine
contrasts = [.1 .98];

for j = 1:length(contrasts)
    stim.contrast = contrasts(j);

    for i = 1 : length (xWidth)
        stim.x.width = xWidth(i);
        %(S) Stimulus
        N = makeNeuralImage(p,stim); % N in Supp. Eq. 1

        %(E) Convolve stimulus with RF to get ...

```

```

% 'stimulus drive' Sup. Eq. 1
E = convolveImage(p,N,p.e.x.width, ...
p.e.theta.width);

%(S) Convolve excitatory drive by inhibitory
% filters for 'suppressive drive'
% Sup. Eq. 2
S = convolveImage(p,E,p.i.x.width, ...
p.i.theta.width);

%(R) Pass total excitation through normalization
% stage to get the population response
R = (E)./(S+p.sigma); % Eq. 1 & Sup. Eq. 3
imshow(R);

% find the maximum value
% [Resp(i,j), max_idx] = max(R(:));
Resp(i,j) = sum(sum(R(:,(length(p.x)/2)-5:...
(length(p.x)/2)+5)));
end
end

%% plot size tuning functions – Fig 2F
maxVal = max(max(Resp(:,1)),max(Resp(:,2)));
figure; hold on
plot(xWidth,Resp(:,1)./maxVal,'b-s','MarkerSize',8,...
'linewidth',1,'MarkerFaceColor','w')
plot(xWidth,Resp(:,2)./maxVal,'r-s','MarkerSize',8,...
'linewidth',1,'MarkerFaceColor','w')

%%V1%%
plot([1 1],[0 0.05],'k:','linewidth',1)
plot([2 2],[0 0.05],'k:','linewidth',1)

```

```

plot ([5 5],[0 0.05], 'k:', 'linewidth',1)
plot ([12 12],[0 0.05], 'k:', 'linewidth',1)

text (1,0.1, 's1', 'color', 'k', 'fontsize',18)
text (2,0.1, 's2', 'color', 'k', 'fontsize',18)
text (5,0.1, 'L1', 'color', 'k', 'fontsize',18)
text (12,0.1, 'L2', 'color', 'k', 'fontsize',18)

plot ([1 1],[0.13 .8], 'k:', 'linewidth',1)
plot ([2 2],[0.13 .83], 'k:', 'linewidth',1)
plot ([5 5],[0.13 .96], 'k:', 'linewidth',1)
plot ([12 12],[0.13 .97], 'k:', 'linewidth',1)

%%MI%%
% plot ([1 1],[0 0.05], 'k:', 'linewidth',1)
% plot ([2 2],[0 0.05], 'k:', 'linewidth',1)
% plot ([5 5],[0 0.05], 'k:', 'linewidth',1)
% plot ([12 12],[0 0.05], 'k:', 'linewidth',1)
%
% text (1,0.1, 's1', 'color', 'k', 'fontsize',18)
% text (2,0.1, 's2', 'color', 'k', 'fontsize',18)
% text (5,0.1, 'L1', 'color', 'k', 'fontsize',18)
% text (12,0.1, 'L2', 'color', 'k', 'fontsize',18)
%
% plot ([1 1],[0.13 .979], 'k:', 'linewidth',1)
% plot ([2 2],[0.13 .99], 'k:', 'linewidth',1)
% plot ([5 5],[0.13 .96], 'k:', 'linewidth',1)
% plot ([12 12],[0.13 .74], 'k:', 'linewidth',1)

set (gca, 'fontsize',14, 'XTick',[0 2 5 12])
set (gcf, 'color', 'w')
legend ('10%', '98%', 'FontSize',10)
box off

```

```

axis([0 13 0 1.1])
xlabel('Stim. size (arb. units)', 'color', 'k')
ylabel('Normalized response', 'color', 'k')

%% compute threshold and plot

% pick the stimulus sizes from our psychophysical ...
% experiment
stim_sizes = [1 2 5 12];

use_sizes_idx = [find(xWidth == stim_sizes(1))...
    find(xWidth == stim_sizes(2))...
    find(xWidth == stim_sizes(3))...
    find(xWidth == stim_sizes(4))];

% duration threshold = criterion / response, Eq. 3 & Eq. 4
Duration_thresholds = ...
    [Criterion(1)/Resp(use_sizes_idx(1),1) ...
    Criterion(1)/Resp(use_sizes_idx(2),1) ...
    Criterion(1)/Resp(use_sizes_idx(3),1) ...
    Criterion(1)/Resp(use_sizes_idx(4),1);...
    Criterion(2)/Resp(use_sizes_idx(1),2) ...
    Criterion(2)/Resp(use_sizes_idx(2),2)...
    Criterion(2)/Resp(use_sizes_idx(3),2) ...
    Criterion(2)/Resp(use_sizes_idx(4),2)];

SI = [1./Duration_thresholds(1,2) - ...
    1./Duration_thresholds(1,1), ...
    1./Duration_thresholds(1,4) - ...
    1./Duration_thresholds(1,3), ...
    1./Duration_thresholds(2,2) - ...
    1./Duration_thresholds(2,1), ...
    1./Duration_thresholds(2,4) - ...

```

```

1./Duration_thresholds(2,3)]

% plot thresholds – Fig 2G
figure
hold on
plot(stim_sizes, Duration_thresholds(1,:), 'b-d', ...
     'MarkerSize', 10, 'linewidth', 1, 'MarkerFaceColor', 'w')
plot(stim_sizes, Duration_thresholds(2,:), 'r-s', ...
     'MarkerSize', 10, 'linewidth', 1, ...
     'MarkerFaceColor', 'w')
set(gca, 'fontsize', 14)
box off

set(gca, 'XTick', [1:12], 'XTickLabels', {'1', '2', '', '', ...
     '5', '', '', '', '', '', '', '12'}, ...
     'fontsize', 14, 'XColor', 'k', 'YColor', 'k')

set(gcf, 'position', [169 160 431 420])
set(gcf, 'color', 'w')
xlabel('Stim. size (arb. units)', 'color', 'k')
ylabel('Threshold (arb. units)', 'color', 'k')
h = legend('10%', '98%', 'FontSize', 10);
set(h, 'EdgeColor', 'k', 'TextColor', 'k', 'Location', 'North')

```

Listing B.3: Convolve function for our model.

```

function [out, xFilt, thetaFilt] = convolveImage...
(p, img, xWidth, thetaWidth)
% [out, xFilt, thetaFilt] = convolveImage...
% (p, img, xWidth, thetaWidth)
%
% Author: Geoff M. Boynton
% University of Washington, Dept. of Psychology
%

```

```

% Adapted from code by Reynolds & Heeger (2009), from
% their paper entitled "The Normalization Model of
% Attention" in Neuron, 61(2), p. 168–185
% Their original code is available from:
% http://www.snl-r.salk.edu/~reynolds/...
% http://www.cns.nyu.edu/heegerlab/?page=software

dx = p.x(2)-p.x(1);
dtheta = p.theta(2)-p.theta(1);

%standard convolution for space (x) dimension:
xc = p.x(ceil(length(p.x)/2));
xFilt = normpdf(p.x,xc,xWidth);
out = dx*conv2(img,xFilt,'same');

%circular convolution for orientation (theta) dimension
thetac = p.theta(ceil(length(p.theta)/2));
thetaFilt = normpdf(p.theta,thetac,thetaWidth);

thetaFilt = repmat(thetaFilt(:),1,length(p.x));
out = dtheta*fftshift(real( ifft( fft(out).*fft(thetaFilt)) ),1);

```

Listing B.4: Neural image for annular gratings.

```

function img = makeNeuralImageAn(p,pN,aN)
% img = makeNeuralImage(p,pN)
%
% Creates a 'neural image' on the axes defined by ...
% p.x and p.theta based on the list of position and ...
% orientation centers and widths in 'pN'.
%
% Author: Geoff M. Boynton
% University of Washington, Dept. of Psychology

```

```

%
% Adapted from code by Reynolds & Heeger (2009), ...
% from their paper entitled ‘‘The Normalization Model ...
% of Attention’’ in Neuron, 61(2), p. 168–185
% Their original code is available from:
% http://www.snl-r.salk.edu/~reynolds/
% Normalization_Model_of_Attention/
% http://www.cns.nyu.edu/heegerlab/?page=software

if ~isfield(pN, 'contrast')
    pN.contrast = ones(size(pN.x.center));
end

if ~isfield(pN, 'range')
    pN.range = [0,1];
end

if ~isfield(pN, 'method')
    pN.method = 'multiply';
end

x = p.x(:)';
theta = p.theta(:);

img = zeros(length(theta),length(x));
%loop through the list of stimulus components
for i=1:length(pN.x.center)
    if isfinite(pN.x.width(i)) %-aN.x.width(i)
        xG1 = (pN.x.width(i))*sqrt(2*pi)*...
            normpdf(x,0-((pN.x.width(i) ...
            +aN.x.width(i))/2),pN.x.width(i) ...
            -aN.x.width(i));
        xG2 = (pN.x.width(i))*sqrt(2*pi)*...

```

```

        normpdf(x,((pN.x.width(i)...
+aN.x.width(i))/2),pN.x.width(i)...
-aN.x.width(i));
        xG = xG1+xG2;
    else
        xG = ones(size(x));
    end
    if isfinite(pN.theta.width(i))
        thetaG = pN.theta.width(i)*sqrt(2*pi)*...
        normpdf(theta,pN.theta.center(i),...
        pN.theta.width(i));
    else
        thetaG = ones(size(theta));
    end

switch pN.method
    case 'multiply'
        subImg = thetaG*xG;
    case 'add'
        subImg = .5*repmat(thetaG,1,...
        length(p.x))+.5*repmat...
        (xG,length(p.theta),1);
    case 'or'
        thetaImg = repmat(thetaG,1,length(p.x));
        xImg = repmat(xG,length(p.theta),1);

        subImg = 1-(1-thetaImg).*(1-xImg);
    end
    img = img+pN.contrast(i)*subImg;
end

img = img*(pN.range(2)-pN.range(1))+pN.range(1);

```

```
%imshow(img);
```

Listing B.5: Neural image for disc gratings.

```
function img = makeNeuralImage(p,pN)
% img = makeNeuralImage(p,pN)
%
% Creates a 'neural image' on the axes defined by ...
% p.x and p.theta based on the list of position and ...
% orientation centers and widths in 'pN'.
%
% Author: Geoff M. Boynton
% University of Washington, Dept. of Psychology
%
% Adapted from code by Reynolds & Heeger (2009), ...
% from their paper entitled ‘‘The Normalization Model ...
% of Attention’’ in Neuron, 61(2), p. 168–185
% Their original code is available from:
% http://www.snl-r.salk.edu/~reynolds/
% Normalization_Model_of_Attention/
% http://www.cns.nyu.edu/heegerlab/?page=software

if ~isfield(pN,'contrast')
    pN.contrast = ones(size(pN.x.center));
end

if ~isfield(pN,'range')
    pN.range = [0,1];
end

if ~isfield(pN,'method')
    pN.method = 'multiply';
end
```

```

x = p.x(:)';
theta = p.theta(:);

img = zeros(length(theta),length(x));
%loop through the list of stimulus components
for i=1:length(pN.x.center)
    if isfinite(pN.x.width(i))
        xG = pN.x.width(i)*sqrt(2*pi)*...
            normpdf(x,pN.x.center(i),pN.x.width(i));
    else
        xG = ones(size(x));
    end
    if isfinite(pN.theta.width(i))
        thetaG = pN.theta.width(i)*sqrt(2*pi)*...
            normpdf(theta,pN.theta.center(i), ...
                pN.theta.width(i));
    else
        thetaG = ones(size(theta));
    end

    switch pN.method
        case 'multiply'
            subImg = thetaG*xG;
        case 'add'
            subImg = .5*repmat(thetaG,1,length(p.x))+...
                .5*repmat(xG,length(p.theta),1);
        case 'or'
            thetaImg = repmat(thetaG,1,length(p.x));
            xImg = repmat(xG,length(p.theta),1);

            subImg = 1-(1-thetaImg).*(1-xImg);
    end
end

```

```
img = img+pN.contrast(i)*subImg;  
end  
  
img = img*(pN.range(2)-pN.range(1))+pN.range(1);
```

