SPATIAL ATTENTION AND PARACONTRAST MASKING

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By
Afife Konyalı
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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

SPATIAL ATTENTION AND PARACONTRAST MASKING

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Visual masking is a powerful methodological tool to investigate the dynamics of sensory processing associated with object visibility and identity. Previous paracontrast masking studies revealed three distinct components that have been proposed to reflect processes at different stages and to be mediated by the distinct interactions within and/or across pathways [1, 2]. The brief and prolonged inhibition components are mainly observed within short and long stimulus onset asynchronies (SOAs) and they have been interpreted as the reflectance of early lateral inhibition and late recurrent inhibition within the parvo-dominated P-pathway. On the other hand, the facilitation typically becomes dominant at intermediate SOAs and the excitatory modulations of sub-cortical structures on the parvo-dominated pathway have been proposed as the underlying mechanism. An important question to address is how attention modulates these components and associated processes. In this thesis, two experiments were designed to understand the effects of attention on the components involved in paracontrast masking. In the first experiment, using an experimental design [3] combined with a contour discrimination task, the set-size was varied to manipulate attention in the spatial domain. The paracontrast masking functions indicated robust brief and prolonged inhibitions. Importantly, the set-size differentially altered these components. An increase in set-size (i.e., attentional load in the visual field) decreased brief inhibition while increasing the prolonged inhibition. In a second experiment, a brightness/contrast matching task was used to understand the effects of attention on the facilitation. Although the paracontrast masking functions showed facilitation at intermediate SOAs and the component was higher for increased set-size condition, these observations were not supported by statistical tests. Taken together, these findings revealed differential effects of spatial attention on the inhibitory mechanisms operating at distinct stages of P-pathway. In the last part of the thesis, an elaborated experimental design was also proposed

to further understand and reveal possible effects of attention on the facilitatory mechanism. Future neuroimaging studies will be informative to understand the neural correlates of attention and paracontrast interaction, and hence the role of attention in object visibility.

Keywords: attention, masking, visibility, temporal dynamics, inhibition, facilitation.

ÖZET

UZAMSAL DİKKAT VE PARAKONTRAST MASKELEME

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Görsel maskeleme, nesne görünürlüğü ve kimliği ile ilişkili duyusal işlemenin dinamiklerini araştırmak için güçlü bir metodolojik araçtır. Önceki parakontrast maskeleme çalışmaları, farklı aşamalardaki süreçleri yansıttığı ve yolaklar içindeki ve / veya yolaklar arasındaki farklı etkileşimlerin aracılık ettiği önerilen üç farklı bileşeni ortaya çıkarmıştır [1, 2]. Kısa ve uzun süreli inhibisyon bileşenleri esas olarak kısa ve uzun uyaran başlangıçlı asenkronlarda (SOA'lar) gözlenir ve bunlar, parvo-dominant P-yolağı içindeki erken-lateral inhibisyon ve geç-rekürent inhibisyonun yansıması olarak yorumlanmıştır. Öte yandan, fasilitasyon tipik olarak orta-düzey SOA'larda baskın hale gelir ve altta yatan mekanizma olarak alt kortikal yapıların parvo-dominant yolak üzerindeki uyarıcı modülasyonları önerilmiştir. Ele alınması gereken önemli bir soru, dikkatin bu bileşenleri ve ilişkili süreçleri nasıl değiştirdiğidir. Bu tezde, dikkatin parakontrast maskelemede yer alan bileşenler üzerindeki etkilerini anlamak için iki deney tasarlanmıştır. İlk deneyde, önceki bir deneysel tasarım [3] kontur ayırt etme görevi ile birlikte kullanılmış ve set-büyüklüğü mekânsal alanda dikkati manipüle etmek için değiştirilmiştir. Parakontrast maskeleme fonksiyonları, güçlü kısa- ve uzun-süreli inhibisyonları ortaya çıkarmıştır. Daha da önemlisi, set-büyüklüğü bu bileşenleri farklı şekillerde değiştirmiştir. Set-büyüklüğündeki bir artış (yani, görsel alandaki dikkat yükünde bir artış), uzun süreli inhibisyonu artırırken kısa süreli inhibisyonu azaltmıştır. İkinci deneyde, dikkatin fasilitasyon bileşeni üzerindeki etkilerini anlamak için bir parlaklık / kontrast eşleştirme görevi kullanılmıştır. Parakontrast maskeleme işlevleri orta-düzey SOA'larda fasilitasyon göstermesine ve bu etkinin set-büyüklüğü fazla olan koşul için daha yüksek olmasına rağmen, bu gözlemler istatistiksel testlerle desteklenememiştir. Birlikte ele alındığında, bu bulgular, uzamsal dikkatin P-yolağının farklı aşamalarında işleyen, inhibisyona dayalı mekanizmalar üzerindeki farklı etkilerini ortaya koymuştur. Tezin

son bölümünde, dikkatin fasilitasyon bileşeni üzerindeki olası etkilerini daha iyi anlamak ve ortaya çıkarmak için ayrıntılı bir deneysel tasarım da önerilmiştir. Gelecekteki nörogörüntüleme çalışmaları, dikkatin ve parakontrast etkileşiminin sinirsel ilişkilerini ve dolayısıyla dikkatin nesne görünürlüğündeki rolünü anlamak için bilgilendirici olacaktır.

Anahtar sözcükler: dikkat, maskeleme, görünürlük, zamansal dinamikler, inhibisyon, fasilitasyon.

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Contents

List of Figures

Chapter 1

Introduction

1.1 Human Visual System

Vision is the most studied modality in all sensory systems. In terms of information processing, the visual system is a great example for the overall organization of sensation besides occupying a large amount of anatomical space in the human cerebral cortex, (around one-third of the whole cortex). As one can infer from the significant amount of visual information processing that takes place in the cortex, the vision also has a survival role and has been considered to be the most informative sense. From low-level to high-level regions (i.e., from retinal ganglion cells until the high-level areas each level integrates various components to analyze more complex elements), the information is transmitted through distinct parallel pathways. These pathways are mainly specialized for different visual attributes.

One can divide the visual system into three main divisions: the eye and retina, lateral geniculate nucleus (LGN), and primary visual cortex and associated areas. The primary input to the visual system is light reflected from objects. Visual information processing starts at the retina, a layer at the back of the eye. The retina contains various cells specialized for visual information processing such as photoreceptors (rods and cones), bipolar, amacrine, horizontal, and ganglion cells.

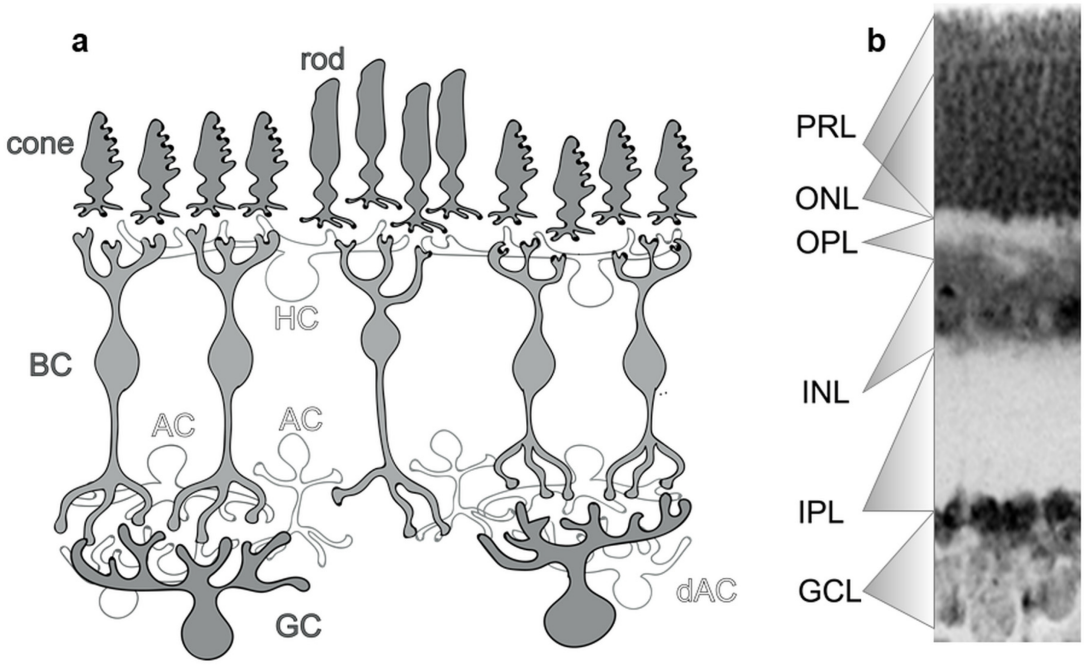

Figure 1.1: The distribution of retinal cells(a) and layers(b) where GC, AC, BC, and HC stands for Ganglion cell, Amacrine cell, Bipolar cell, and Horizontal informational cell, respectively. Retrieved from [4]

At the retina, the light is transduced into a signal that the nervous system can interpret, action potentials (Figure 1.1). After light arrives at the back of the eye (photoreceptors-level), it is transduced into action potentials by photoreceptors (phototransduction). There are two types of photoreceptors: rods and cones. While rods are specialized for dim light, cones are good at color vision. There is inhomogeneity in the distribution of photoreceptors over the retina. Most of the cones are located at the fovea, a small specialized part of the retina that is well-known as a base of sharp vision, whereas only a small proportion of the rods are located here. On the other hand, most of the rods and only a small number of cones are placed at the peripheral regions of the retina. After phototransduction, the information is further transmitted to either ON or OFF bipolar cells that are differentiated based on their responsiveness to the presence or absence of light. All photoreceptors react to light by hyperpolarization. ON bipolar cells convert the sign of the photoreceptor reaction while OFF bipolar cells conserve the sign of the activation produced by photoreceptors. Accordingly, ON bipolar cells increase their activation in response to light, while OFF bipolar cells increase

their activation in the dark situation (i.e., light-off). Bipolar cells transmit the information to ganglion cells which are the exit points from the retina since their axons create the optic nerve carrying the information to LGN and visual cortex.

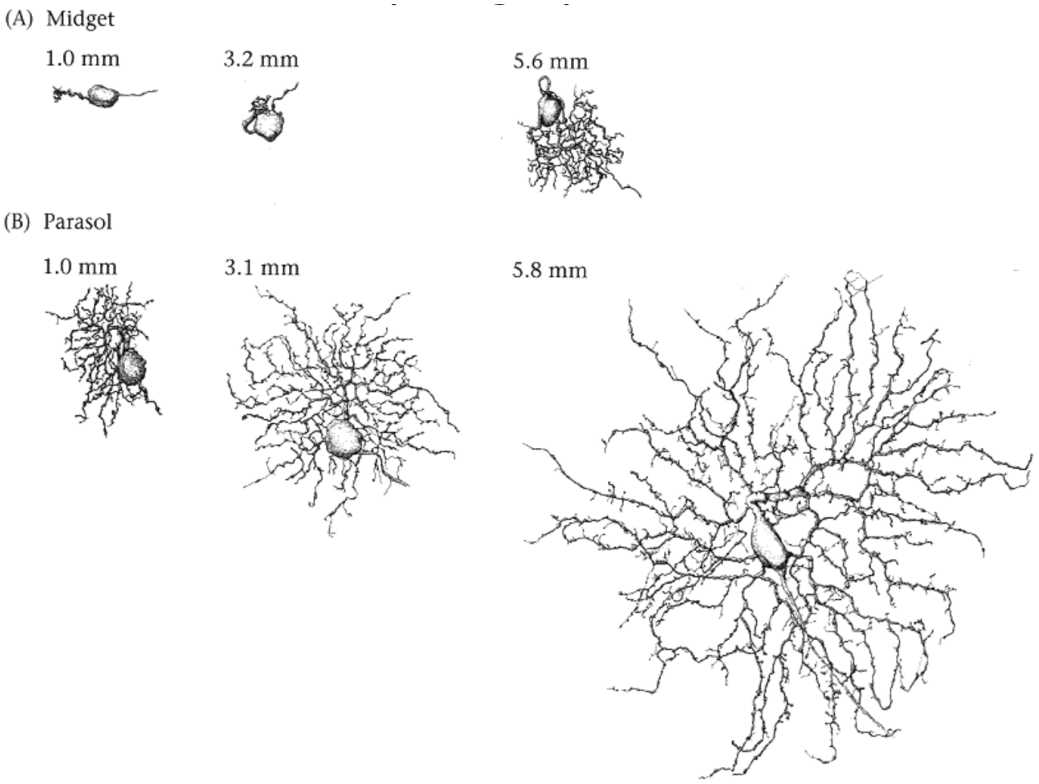

Figure 1.2: The relative sizes of exemplar M-Parasol and P-Midget cells. Retrieved from [5]

Like bipolar cells, retinal ganglion cells have distinct classes of ON and OFF cells according to their responses towards the light. Even though many retinal ganglion cells (RGCs) create action potentials even in darkness, the frequency of action potentials that they produce increases or decreases with increased light intensity for ON and OFF retinal ganglion cells, respectively. Each RGC is responsive to light falling into a specific area in the retina. This "responsive area" defined uniquely for each RGC is named as the receptive field. Each receptive field has a center and surround region responding in a counteracting way to the light. RGCs are named based on the responsiveness of their center region to the light.

Retinal ganglion cells are also categorized into two main groups, M-parasol

cells and P-midget cells, based on their overall shape, response profile, and the pathway that they form. There are other types of retinal ganglion cells projecting to the koniocellular layer of LGN and contributing to color perception. Since M-cells and P-cells create two main pathways of visual perception in the brain, we will focus on these cells.

As shown in Figure 1.2, having a larger cell body and longer/more dendrites, M (parasol) cells are quite bigger than P (midget) cells. 5% of the total population of retinal ganglion cells in the cortex consists of M-cells while 95% of the RGCs consists of P-cells. The conduction velocity of M-cells is faster since their axons are highly myelinated, and their receptive fields are larger than P-cells. As one can easily infer from these properties, M-cells have been shown to mainly contribute to motion and depth perception, but not to color perception. However, P-cells are specialized for fine-tuned information through their small receptive field and slow but sustained response time compared to M-cells. Thus, it is reasonable that P-cells code object-based information such as shape and color. Starting from the retina, M- and P-cells constitute the origin of two parallel processing pathways up to high-level cortical areas.

Based on their activation profiles, these two main cell types (M- and P-cells) have transient and sustained responses, respectively. When the stimulus duration is long enough, it is shown that the transient M-cells get activated as the stimulus begins but they decay faster, even before the stimulus offset. However, the sustained P-cells get activated not at the onset of the stimulus, but after a time. The activity of the sustained cells lasts longer, and their decay occurs gradually [16]. As indicated in the previous literature [8, 16], the sustained cells, as a complementary behavior to transient cells, are tuned to high spatial and low temporal frequency.

Figure 1.3 displays the visual system comprehensively, starting from the retina up to the high-level cortical areas. As seen in Figure 1.3, parasol(M) and midget(P) cells transmit visual information to different layers of LGN and V1(4Cα and 4B layers for M-cells; 4Cβ layer of V1 for P-cells). Then, the signals are projected either to the thick stripes of V2 and MT (medial temporal area) or

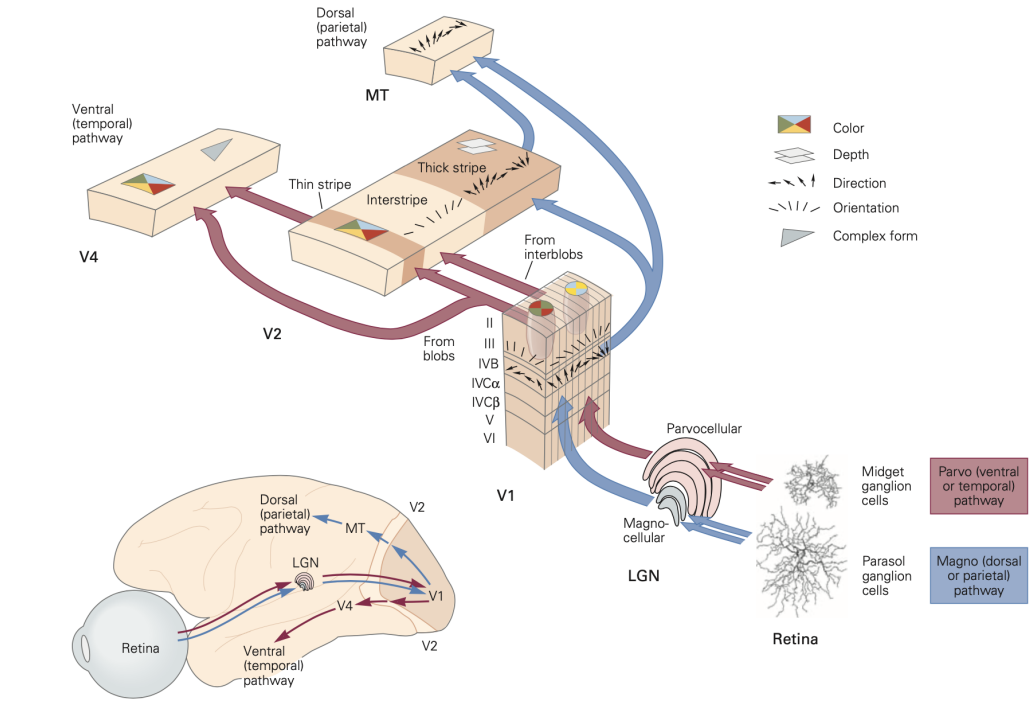

Figure 1.3: Illustration of the Parvo-dominated ventral pathway and Magno-dominated dorsal pathway, starting from the retina and going until higher-visual areas after stopping by at the LGN. Retrieved from [6]

thin and pale stripes of V2 and V4. Starting with M-parasol and P-midget cells, these pathways are well-known processing pathways and are called the Magno-dominated dorsal and Parvo-dominated ventral pathways, respectively.

The Dorsal and Ventral pathways mainly process different aspects of visual information. For instance, including areas specializing in motion and location perception such as MT, the dorsal pathway processes visual information based on the direction and speed of the motion and is tuned for binocular disparity. Therefore, the dorsal pathway is also named the "where" pathway, since it is responsible for the processing of the locational information in the retinal image.

On the other hand, the ventral pathway (also known as the "what" pathway), starting with P-midget cells and traveling through specified layers of LGN, V1, V2, V4, and up to the IT (inferior temporal cortex) is specialized for color, shape perception and object recognition.

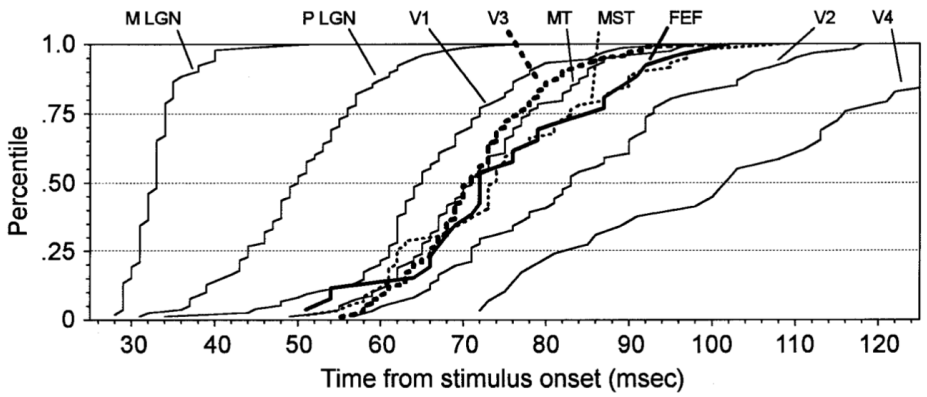

Figure 1.4: The cumulative response profiles of each visual area located at different stages of processing (i.e., low- and high-level visual areas). The percentage of the neurons significantly responding is shown as a function of time after stimulus onset. Retrieved from [7]

Up to this point, the hierarchical and feedforward organization of the visual system, which is based on their receptive field profile (being less or more specific), is described. On the other hand, there are also feedback connections within a level or from higher-level areas that may be related to the attentional modulation or perceptual context [17]. Even though it is well accepted that both feed-forward and feedback connections play a crucial role in perception, there is still no consensus on the exact role of each of these connections [18]. The role of feedback connections is emphasized by the findings of the two-way communication between V1 and higher-level visual areas [9]. Various studies have also investigated the functional roles of feedback connections in different visual attributes [19, 20, 21, 22, 23]. Since the role of feedback connections on visual masking and attentional processes are more related to this thesis, we will focus on that part.

The basic differences between M- and P-cells, in terms of their response timing profile and temporal features, are preserved through the dorsal and ventral pathways. This fact is revealed by measuring responses of each area from anesthetized macaque monkeys and various visual stimulation flashing for 500 ms [7]. Figure 1.4 shows the response latencies of neurons located at different locations of the visual system. As shown by onset latencies, the magnocellular pathway has overall shorter latencies compared to the parvocellular pathway. This difference in activation profiles and onset latencies has been at the core of theoretical and

experimental work on visual masking.

1.2 Visual Masking

To understand this complex nature of visual perception, a phenomenon called "visual masking" has been used as a powerful investigative tool. Visual masking refers to the reduction in the visibility of a stimulus (target) due to the presentation of another (mask). As Kahneman [24] pointed out in his article, Pieron is the first scientist who used visual masking as a term in 1925. Kahneman [24] further added that using masking terminology was "revived" after Boynton and Kandel [25]. Before the term visual masking was established, Stigler [26] is credited to conceptually and experimentally define terms of metacontrast and paracontrast (types of masking further explained below), even though there were preliminary studies on metacontrast and paracontrast masking [27, 28, 29](for further information see Breitmeyer and Öğmen [8],Chapter 1).

As mentioned in the previous section, there is inhomogeneity in the distribution of the photoreceptors over the retina. Due to this inhomogeneity, we often, even 3 or 4 times per second, make saccadic eye movements to focus the image on the fovea, which is a retinal area specialized with a high-density of receptors. However, we do not perceive any distortion in the image in our perception. It is supposed that visual masking acts as a mask for small changes during saccades and provides smooth image processing (Ağaoğlu [30], p.2).

According to another view on how visual masking is used naturally in the human visual system, the visual masking regulates the availability of information by manipulating the storing duration during the transmission between memory components. As detailed in the next chapter (see 1.2.5 Attention and Memory), in terms of the registration of the visual information to the memory system, iconic memory is the first station with very high capacity in terms of the number of icons handled at a time but only for a short time (less than 1000 ms). Coltheart [16] identifies three ways of persistence of a stimulus after its physical offset. These

are neural persistence, visible persistence, and informational persistence. Neural persistence refers to the visual system starting from photoreceptors and continuing with LGN and visual cortical areas (see 1.1 Human Visual System). Visible and informational persistence, as two main components of the iconic memory, refer to different components of the visual system that store various aspects of the presented visual stimulus. While visible persistence refers to keeping a residual image of a stimulus, informational persistence refers to keeping the informational components of the stimulus by the visual system. Visible persistence suggests that a scene stays available for a while, and it requires time to decay [16]. The digital cameras create blurry images when recording motion due to fast-changing images. However, we do not perceive such a blur while seeing moving objects. In fact, there is a clear and sharp image/perception even in motion-related scenes. The reduction of suggested blurriness is known as motion-deblurring and it is suggested that through the mechanism of masking the visual system eliminates the unwanted residuals to create sharp images and to deblur the image during motion [31, 30].

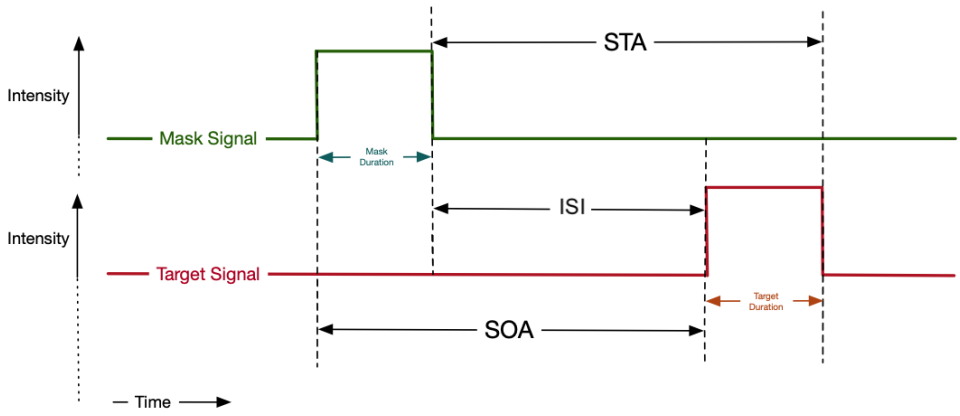

Figure 1.5: The signal intensities and relative durations of mask and target stimuli in a typical forward masking (paracontrast) paradigm. Naming of time differences between stimuli are displayed. STA, ISI and SOA refer to Stimulus-Termination-Asynchrony, Interstimulus-Interval and Stimulus-Onset-Asynchrony, respectively.

A basic visual masking paradigm has two types of stimuli: target and

mask. Target is the stimulus that observers are expected to respond to and generally there is a time interval between mask and target. Mask stimulus changes/moderates the visibility of target based on some parameters. To manipulate the amount of masking, the relative timing between target and mask is varied. In the literature, different metrics were used to systematically change the relative timing. As indicated in Figure 1.5, either interstimulus-interval (ISI) which represents the time between the offset of one stimulus and onset of the other, or stimulus onset asynchrony (SOA) which is defined as the time difference between the onsets of target and mask stimuli. Visual masking paradigms were classified based on physical stimulation and characteristics of target and mask.

Based on the relative timing between two stimuli, masking has three types: forward, backward, and simultaneous masking. In forward masking, the mask stimulus is presented first, and the target is presented afterward. Conversely, backward masking is the type of masking in which the target precedes the mask. As the name infers, when mask and target have a common onset, the masking is called simultaneous masking (see Figure 1.6). The amount of masking is expected to be large in this type of masking because both stimuli enter the system at the same time, and it is likely that they interact with each other at every stage of the visual processing.

Taking other physical features of a mask and target into account, the types of visual masking can be divided into two categories, masking by light and pattern masking. Kahneman [24] denotes that segregation occurred to refer to the spatial overlap between the mask and, target stimuli. In the masking by light, a flashing area that is illuminated uniformly is used as a mask. The mask, in masking by light, completely contains the contours of the target stimulus [24]. However, this is not strictly determined in the pattern-masking. Pattern masking is defined by Breitmeyer and Öğmen [8] as both mask and target stimuli "consist of spatially patterned forms and contours". Pattern masking consists of three categories, paracontrast/metacontrast, masking by noise, and masking by structure (see Figure 1.7). In all of these masking types, the target shape or features may be different, but the mask properties determine the type of the masking. When

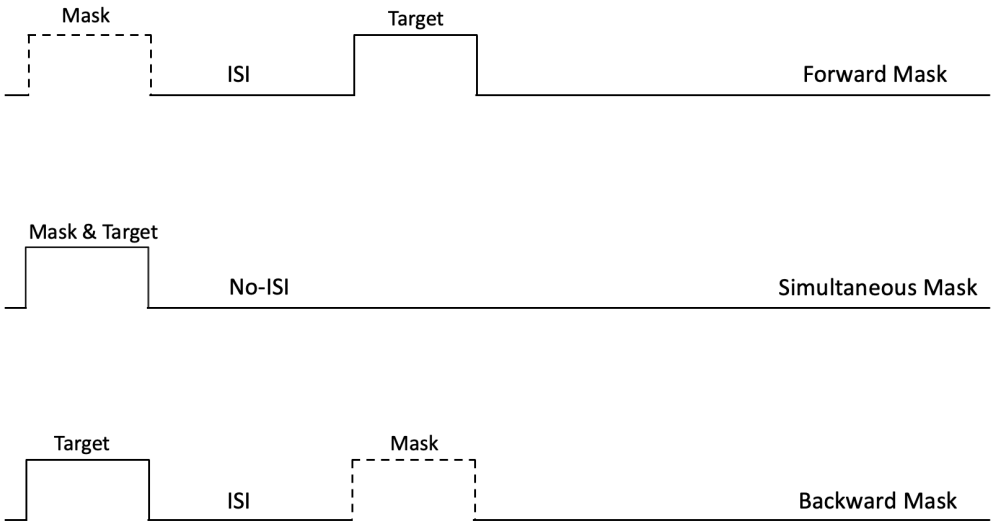

Figure 1.6: Visual masking types based on the relative timing (i.e., onset timing) of the stimuli.

the mask is composed of randomly distributed dots over an area overlapping with the target (e.g., white noise), this type of visual masking is called masking by noise. Secondly, if the mask stimulus has a pattern/shape or is composed of some structural features of the target, it is called masking by structure. Paracontrast/metacontrast are special types of pattern masking in which mask and target both have a form and do not overlap spatially. The paracontrast and metacontrast also correspond to forward and backward masking, respectively. However, Kahneman [24] indicates that studies in the literature, at that time, used metacontrast to refer to non-overlapping masking paradigms regardless of the order in between target and mask.

Metacontrast masking has been commonly studied and attracted more attention due to its counterintuitive nature. There are a few studies in the literature focusing on paracontrast. Therefore, compared to metacontrast, the principles and mechanisms underlying paracontrast are poorly understood.

In visual masking paradigms, the visibility of the target, or the performance in the task corresponding to the target stimulus, is moderated by the stimulus

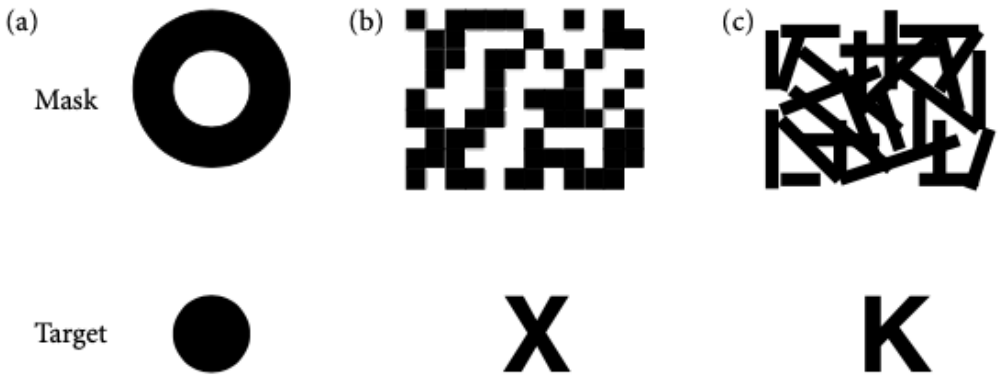

Figure 1.7: Exemplars of mask and target stimuli for different types of pattern masking. Paracontrast/metacontrast (a), masking by noise (b) and masking by structure (c). Retrieved from [8]

onset asynchrony (SOA). This relation is defined as a masking function in which decreasing visibility refers to the masking effect. Visibility in a masking function (or performance) is measured either by the accuracy or by the response time. As pointed out by previous research [8], the low-level stimulus parameters (e.g., luminance, size, duration, target-mask separation) and criterion content (e.g., visibility rating, luminance matching, forced-choice pattern discrimination) can alter the morphology of the masking function. There are several studies in the literature studying the effects of each of these variables on the masking function [1, 2, 32, 3, 33, 34]. In the literature, masking functions are classified based on the specific morphology. Typical unimodal masking functions are monotonic (type A) and non-monotonic (type B) while there are also bimodal and multimodal masking functions as shown in Figure 1.8 [8]. Graphs in Figure 1.8 show target visibility in response to the time difference between target and mask. As expected, the target visibility and masking strength (i.e., the reduction in target visibility) are inversely proportional while the proportionality constant is 1 which means that target visibility and masking strength are inverse variables with respect to multiplication (i.e., masking strength=1/(target visibility)).

Since the x-axis represents the time difference between target and mask stimuli, in these figures and generally in the literature, 0 point refers to presenting them simultaneously and, conventionally, negative values refer to mask being presented

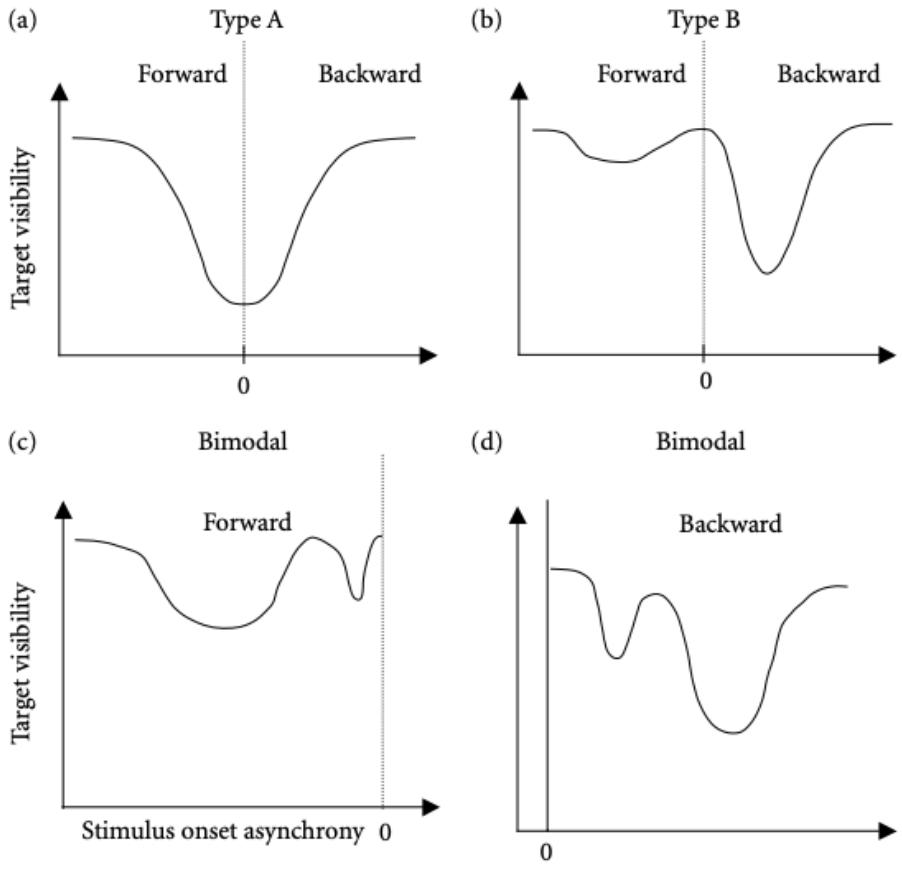

Figure 1.8: Functions of various visual masking functions. Each graph shows target visibility (which equals 1/masking effect) as a function of SOA. Unimodal (a) Type A, (b)Type B functions and bimodal masking functions (c-d) are presented. Retrieved from [8]

before the target and vice versa for the positive values. As time separation between the target and mask increases, the masking effect decreases, so the target visibility increases again to the baseline.

As seen in the figure, the Type-A (monotonic) function makes the mask stronger when the mask and target stimuli get closer in time. This type of masking can be explained by the confusion hypothesis which states that the closeness of mask and target may cause difficulty to perceive the target as an independent and individual item/stimulus so there might be confusion between stimuli causing masking effect [35]. Thus, this kind of explanation can account for the monotonic

masking function, but it cannot explain Type-B (non-monotonic) masking function since Type-B masking function does not refer to bigger masking strength as SOA gets closer to zero.

1.2.1 Common-Onset Masking

Common-onset masking is a variation of backward masking in which the onsets of stimuli are the same, but the mask is constantly presented even after the target presentation. In a study by Di Lollo, Enns, and Rensink [9], a combination of four-dot masking and common-onset paradigm was introduced, and the masking theories based on the feed-forward activity in the visual system were claimed to be insufficient to explain these masking types. The authors emphasized that "re-entrant" signals are crucial for perceptual processing which are relatively underestimated by the former theories. Accordingly, they proposed a new notion called "reentrant theory of perception" focusing on the involvement of reentrant signals in perception by developing a computational model of object substitution (CMOS) [9]. Their reference point is the feedback projections throughout the brain which are also present and salient in the visual system. The theory is also known as object substitution theory since it explains the masking as a result of object substitution in the visual system. Object substitution in the context of common-onset masking (backward masking) is explained as the mismatch between incoming (feedforward) information of the mask which has a long-duration and the feedback information (re-entrant signals) about the flashed target. Object substitution theory is differentiated from others due to the crucial role of attention. In the experiments, a common-onset masking paradigm with the various number of set-sizes is used (1-to-16). In a typical experiment, the masking patterns/functions (masking strength depending on only-mask duration) changes as set-size (potential target stimuli) is increased. Only when the mask duration is bigger than that of the target, as set-size increases from one to sixteen, the masking effect gets stronger. As shown in Figure 1.9, the effects of masking duration become stronger as the set-size increases. They suggested that these differential effects of mask duration are mainly due to the distribution of attentional resources

in the spatial domain. According to this explanation and hypothesis (i.e., object substitution theory), an increase in the set-size distributes attention to several locations. Thus, it takes more time to allocate attention when the set-size increases, and this leads to a stronger masking effect. On the other hand, when the set-size is one, the target "pops-out" and attention is intrinsically captured by the target which decreases the masking effect. Thus, the object-substitution theory claims that there is an interaction between attention and masking mechanisms.

After a series of experiments, they suggested that two different mechanisms contribute to the masking effect: a former component affected by physical properties such as contour processing and a later component affecting masking strength based on the set-size. These components refer to the lower-level processing and the higher-level feedback modulation (i.e., attention), respectively. The latter one is also named as "higher-level object substitution" and defined as the main process for conscious visual perception [9].

Several other studies proposed that this theory and the interaction between the two mechanisms not only apply to common-onset masking [9, 36] but also explain other masking types such as metacontrast [37, 38, 3]. However, the psychophysical findings are contradictory. While some studies provide support for the object-substitution theory and hence, the interaction between masking and attention [9, 36, 37, 38], others pointed out that the interaction between masking and attention may be due to confounding factors such as the ceiling/floor effects in masking functions [33, 3].

1.2.2 Metacontrast Masking

In both metacontrast and paracontrast, there are two main types of experimental tasks used extensively in the literature [1, 2]; contour discrimination task and contrast matching task. In the contour discrimination task, there is a deletion on a side of the target and the task is to determine the deleted side. In the contrast matching task, using a staircase procedure with a comparison stimulus, percieved brightness of the target is calculated.

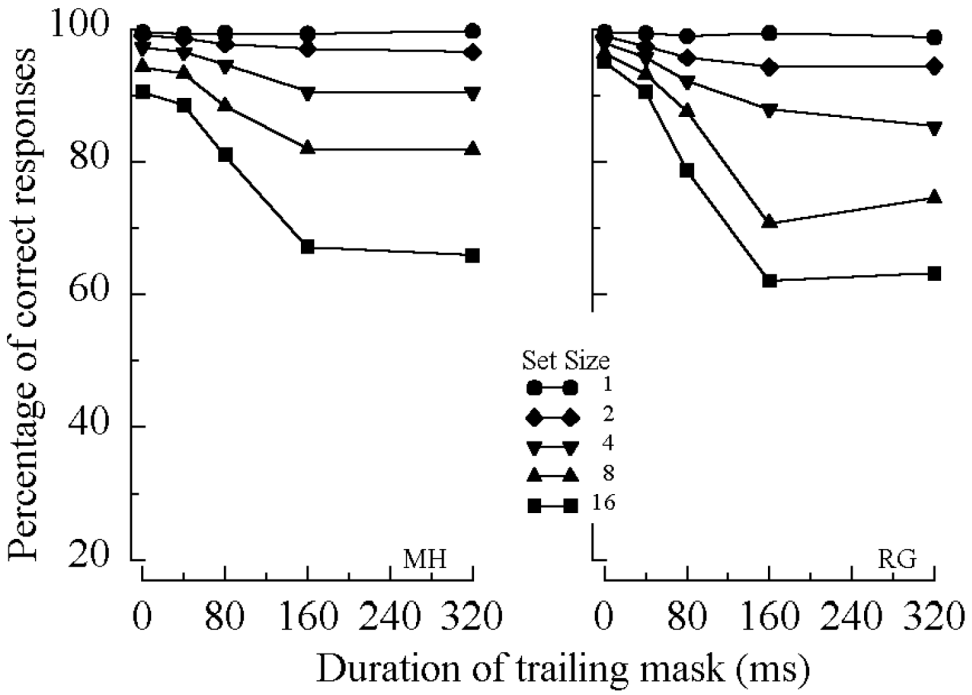

Figure 1.9: The plots showing the results of common-onset masking paradigm with different set-sizes.Each plot displays percentage of correct responses as a function of mask-duration after target display is disappeared. Different curves refer to different set-sizes, various numbers of possible target stimuli. Results from two participants are shown on the left and right. Retrieved from [9]

Metacontrast is a special type of backward masking in which the mask does not spatially overlap with the target. Metacontrast masking is, typically, characterized by the Type-B non-monotonic (U-shaped) masking function. As seen in Figure 1.10, the Type-B metacontrast masking function shows strong masking effects at intermediate SOA values while showing a very weak masking effect at short and long SOA's, for backward masking. As mentioned in the previous sections, the perceptual task and criterion can modulate the masking function. Breitmeyer and Öğmen [8] indicate that reduction in target brightness, deletion in target contour, and suppression of the target figural identity are exemplars of tasks yielding distinct Type-B metacontrast masking function. On the other hand, other types of masking functions can also be observed (e.g., Type-A, see also Figure 8). Such studies are based on different types of tasks that use reaction time or simple detection, respectively [39, 40]. Metacontrast masking has

also been used as a powerful investigative tool due to its interesting and replicable nature, easy to study and characterized function (U-shaped/non-monotonic masking function), and its interaction with other high-level cognitive processes.

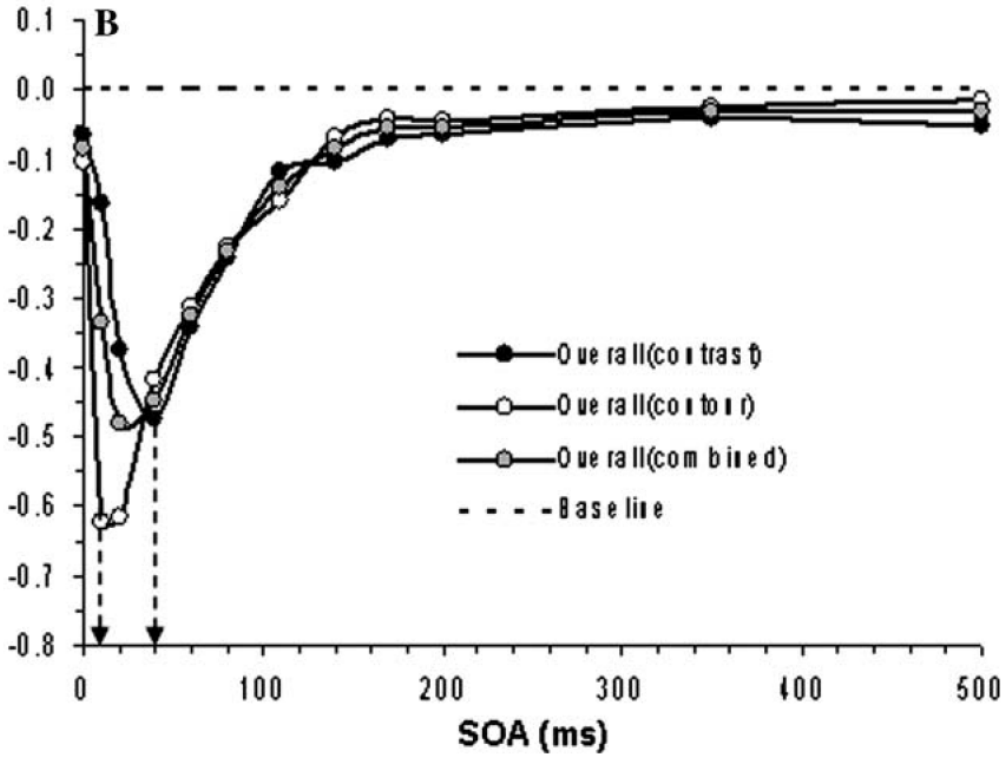

Figure 1.10: Log Relative Visibility as a function of SOA. Showing the results of metacontrast masking experiments for averaged M/T conditions. Different data curves are representing contour judgement and contrast judgement experiments in addition to combined data for all conditions. Retrieved from [1]

Breitmeyer and his colleagues [8] investigated the temporal dynamics of both meta- and para-contrast masking using two different tasks, based on contour discrimination or surface brightness (i.e., contrast). Furthermore, two separate cortical streams, Boundary-Contour-System (BCS: which corresponds to P-interblobs) and Feature-Contour-System (FCS: which corresponds to P-blobs), are suggested to process information for contour and surface, respectively. In their study [1], they reported that there is a distinction, as hypothesized, between contour and contrast processing in masking which is parallel with the cortical dissociation between contour and brightness processing for both meta- and paracontrast. They

also used a model-driven, RECOD model, approach to build specific hypotheses based on this experimental design. Since the RECOD model suggests that there is a dual-channel transmission (see Section 1.2.4.1 Neural-network models adopting overtake and dual-channel activation hypotheses) of the information through visual system and the interaction between and within these channels lead to visual masking, the authors suggested that the surface and contour properties of a stimulus are being distinctively processed within these retino-cortical pathways. They expected to observe a dissociation between masking functions of contour discrimination or contrast matching tasks.

In Figure 1.10, the metacontrast functions show that contour and brightness matching tasks lead to distinct optimal SOAs, even though the overall U-shape of the Type-B metacontrast masking is preserved. These findings suggest that contour processing is faster than contrast(surface) processing which supports the predictions of the RECOD model on metacontrast masking [1]. Section "1.2.4 Recent Theories and Models of Visual Masking" explains the most-common theories on the underlying mechanisms of visual masking. After the RECOD model is introduced, these results will be revisited.

In the previous subsection, it was mentioned that there have been contradictory findings of the asserted relationship between attention and masking. A recent study by Agaoglu, Breitmeyer, and Ogmen [3] further investigated possible interactions between metacontrast masking and attention by avoiding the ceiling/floor effects which are claimed to be the reason (i.e., confounding factor) for the data showing interaction. They used set-size in the visual field as a critical factor to manipulate attention. The experimental design included randomly oriented bars with a set-size of 2 or 6 located on an imaginary circle around the fixation. Once the target bar and distractor bar(s) were displayed for 10 ms , the mask ring around the location of the target bar was presented for 10 ms. The task was to determine the orientation of the target bar by adjusting the orientation of the response bar which has a random orientation for each trial and is presented at the center. The authors used "statistical modeling of response errors" to analyze the data. They suggested several statistical models corresponding to different

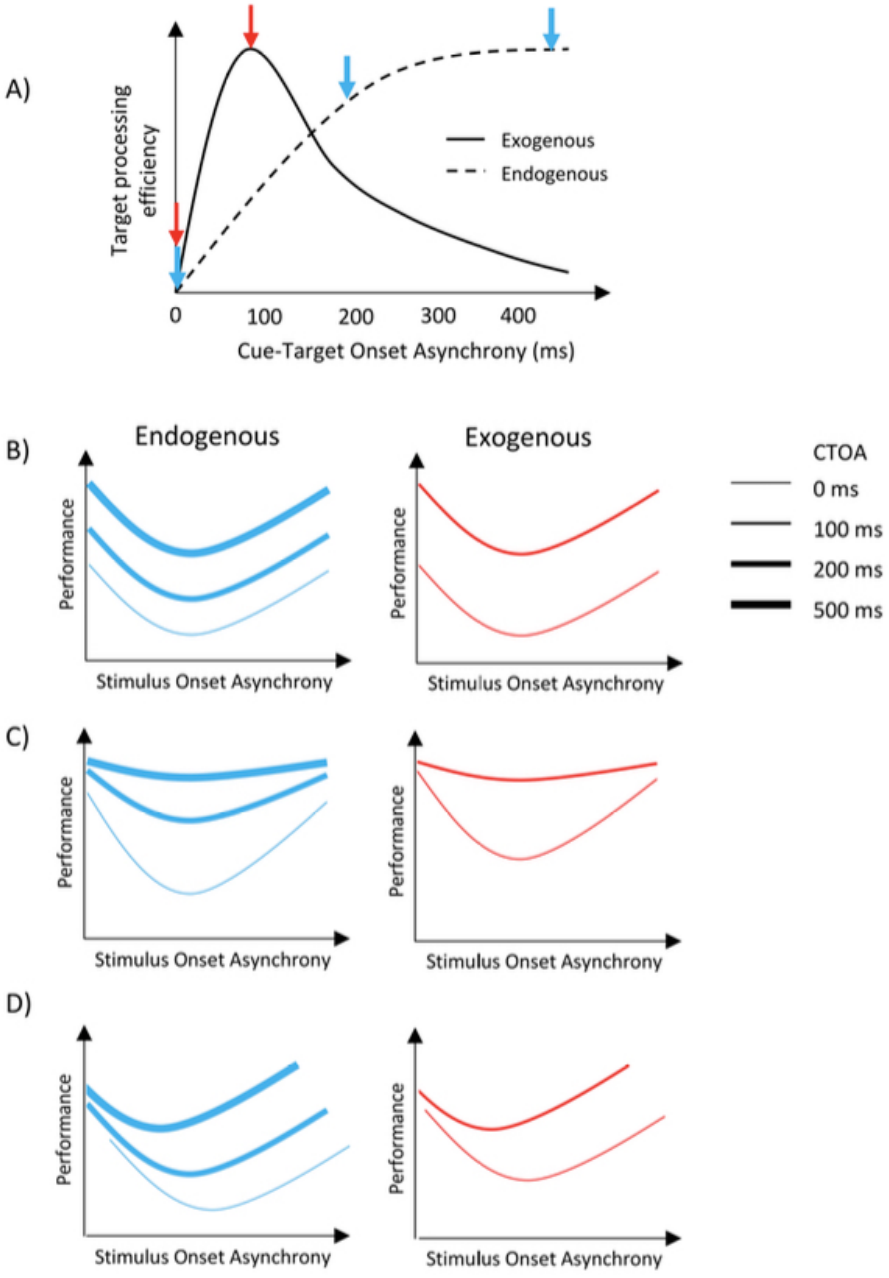

Figure 1.11: **A)** Illustrations of the well-known effects of cueing types (exogenous or endogenous) as a function of Cue-Target onset asynchrony. **B)** shows an expected performance in the metacontrast masking experiment when attention and masking do not interact. **C)** and **D)** show possible performance graphs in the metacontrast masking experiment when attention and masking interact. Retrieved from [10]

theories (with or without interaction etc.) and tested how the outcome of the models explains and overlaps with the behavioral data. Based on these analyses, they concluded that there was an overall performance difference between set-size groups (i.e., the main effect of spatial attention) rather than the interaction between masking and attention processes [3].

In a follow-up study, they used a similar design but did not use set-size to manipulate attention [10]. Instead, they used cue-based attentional manipulation based on endogenous and exogenous cues due to the possible confounding factors of controlling attention by set-size. One of these factors is the dual-role of mask stimulation acting both as a cue (i.e., defining the target location) and as a mask. Therefore, they added a cue to specify the target location and used mask stimuli for both target and distractors. Figure 1.11 shows possible results for several experimental conditions for both in case of interaction (Figure 1.11 C-D) and no interaction (Figure 1.11 B). The authors also analyzed the statistical distribution of the response errors. The findings supported that metacontrast masking and attention do not interact not as hypothesized by common-onset masking theory, but as expected in Figure 1.11-B [10].

1.2.3 Paracontrast Masking

Paracontrast is a special type of forward masking in which target and mask do not overlap spatially but are very close in space. As mentioned before, the paracontrast masking function can be affected by stimulus parameters and criterion content. The experimental task, size of the stimuli, the space between stimuli, their luminance, SOA between target and mask, the background luminance, and presentation duration of target and mask are some of the critical variables that can modulate paracontrast masking function. Therefore, every parameter should be studied delicately and carefully to differentiate its effect on the function. Even though most of the parameter remains to be studied for further understanding, some of the previous studies focused on characterizing the paracontrast masking functions. For example, the space between target and mask was shown to be

one of the critical variables that change the paracontrast masking function. It is indicated that as the target and mask become closer (but still non-overlapping) spatially, the masking effect becomes more robust [2].

In contrast to the findings on metacontrast masking, it is indicated that the performance on tasks such as simple detection or choice RT (target localization) is affected by masking in paracontrast. Since paracontrast results show that RT increases significantly as SOA approaches 0, it rejects the theory that sensory-motor responses are generated by a single sensory-motor pathway not interacting with masking. Because, according to the metacontrast results showing the dissociation between RT and target visibility, it was assumed that RT generating system is immune to masking. Öğmen and his collages focused on this differentiation and explained it from the point of view of the RECOD model (will be explained in detail, later) on both para- and metacontrast [13]. They suggested several hypotheses on task-based dissociation on the masking effect and tested whether this dissociation reflected the characteristics of the neural system (such as the differentiation between where and what pathways) or the timing of stimuli and/or corresponding activity of transient and sustained channels. They concluded that the dissociation is not caused by the immunity of neural pathways to masking. Rather, it is due to the timing of the interaction between sustained and transient channels (see Figure 1.22). To reach this conclusion, they first made a simulation of the experiment based on the RECOD model and then did separate experiments for target visibility and target localization to check whether they were in line with the simulated data and supported the model's predictions or not. It is reported that paracontrast masking was insensitive to any disassociation between target localization and visibility.

Similar to metacontrast, both Type-A and Type-B masking functions are possible for paracontrast, depending on the task. It was shown that the Type-A function for paracontrast is produced when the detection task is used [41]. On the other hand, perceived brightness (contrast) judgment tasks may result in Type-B paracontrast masking function [42, 43, 44]. When perceived brightness/contrast

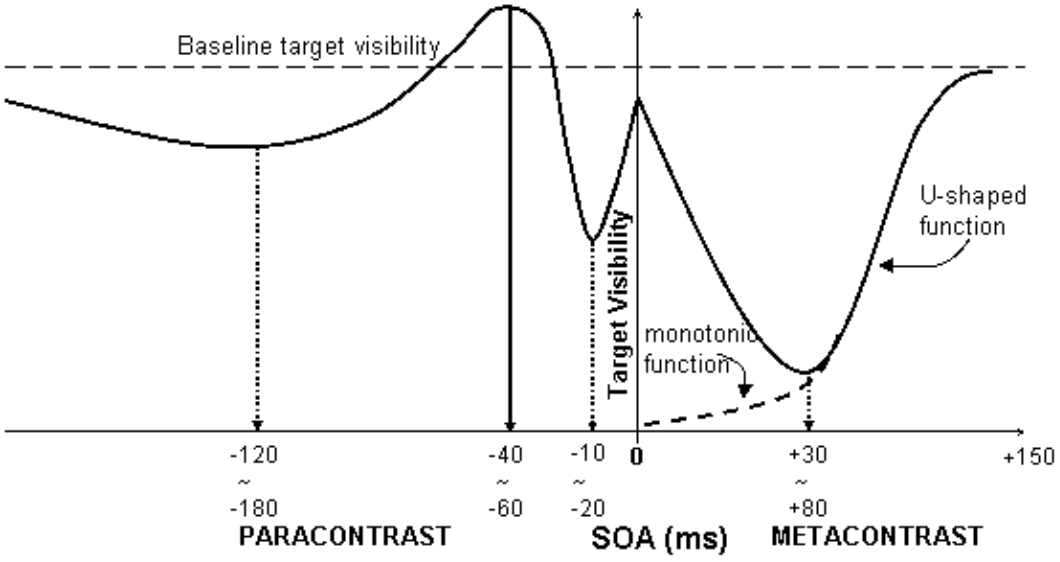

Figure 1.12: Exemplar Type-B (non-monotonic) paracontrast and metacontrast masking functions. Retrieved from [11]

is used as the experimental task, Type-B (non-monotonic) paracontrast masking function is typically reported [2, 1](see Breitmeyer Öğmen [8] for further references). Furthermore, Kolers Rosner [43] obtained type-B paracontrast under dichoptic stimulation, suggesting the involvement of higher-level centers (i.e., cortical areas) in the interaction of mask and target. As seen in this difference between masking functions for various experimental tasks, task and stimuli parameters, and "criterion content", emphasize that the dimensions of stimuli used by the participant to judge are highly important factors affecting the masking function/effect. Bachmann and Francis [22] further hypothesized that criterion content may be the cause of individual differences in masking research since each participant may focus on a different kind of information and hence a different type of function may be generated. Also, Breitmeyer et al. [1] pointed out that task requirements and criterion content can modulate both metacontrast and paracontrast masking functions.

The morphology of the Type-B paracontrast masking function is complicated than the typical Type-B metacontrast masking function which is characterized by

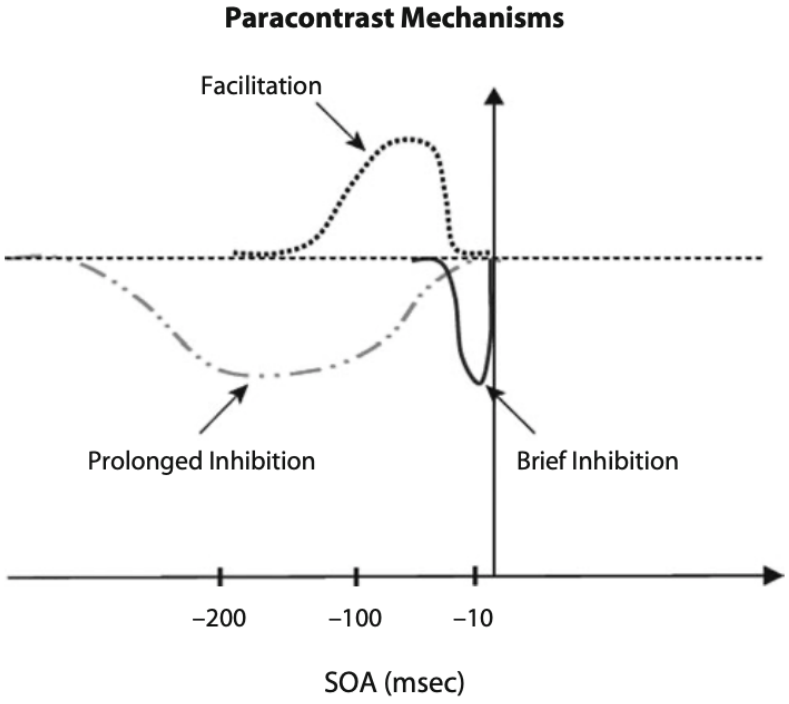

Figure 1.13: Schematic representation of three components of paracontrast masking. Retrieved from [2]

its U-shape (maximum masking effect at intermediate SOAs). Unlike metacontrast, paracontrast masking may reach its local extremum at three different SOAs one of which can lead to facilitation in the target visibility. A typical/generalized non-monotonic (Type-B) paracontrast masking function is presented in Figure 1.12. Even though the functions of the contour discrimination and contrast matching tasks indicate that the strength of local peaks change based on several variables such as criterion content, experimental task, and M/T ratio; in a typical paracontrast function, a robust inhibition is observed at short SOAs around 20 ms, another inhibition becomes dominant beyond 100 ms of SOA, and a facilitation component typically peaks around 60 ms of SOA=40 or SOA=60 (see also [1]). In accordance with the common usage, the inhibition at the small SOA's is named as the brief inhibition, and the inhibition at the bigger SOA's is named as the prolonged inhibition while the increase at the visibility of the target at intermediate SOA's is named as facilitation.

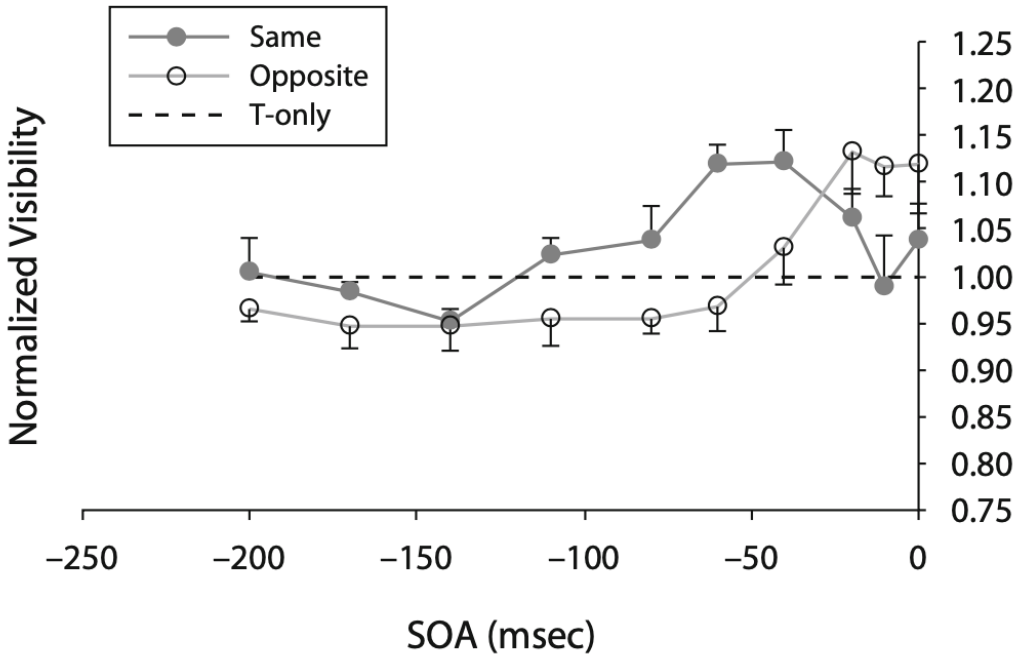

Figure 1.14: Results of contrast polarity experiment. Same refers to target and mask stimuli having the same luminance value (so the same contrast polarity, both lighter than the background); opposite refers to the condition that target and mask having opposite contrast polarity(target still had the same luminance value with other condition but mask was darker than the background). Retrieved from [2]

Fragmenting into components, Breitmeyer et al. [1] depicted a schematic representation of these paracontrast components (Figure 1.13). They further proposed that each component is generated by a different neural mechanism. As shown in Figure 1.13 , contour and contrast tasks generate different components of the paracontrast function. Both brief and prolonged inhibitions become dominant for contour discrimination task, while paracontrast function in contrast matching task has a clear facilitation component with no/or small inhibition components.

Another study by Kafalıgönül et al. [2] systematically examined these components of paracontrast by manipulating the spatial separation between target and mask. The target-mask spatial separation was manipulated to test the hypothesis that facilitation in the paracontrast was mainly caused by lateral excitatory

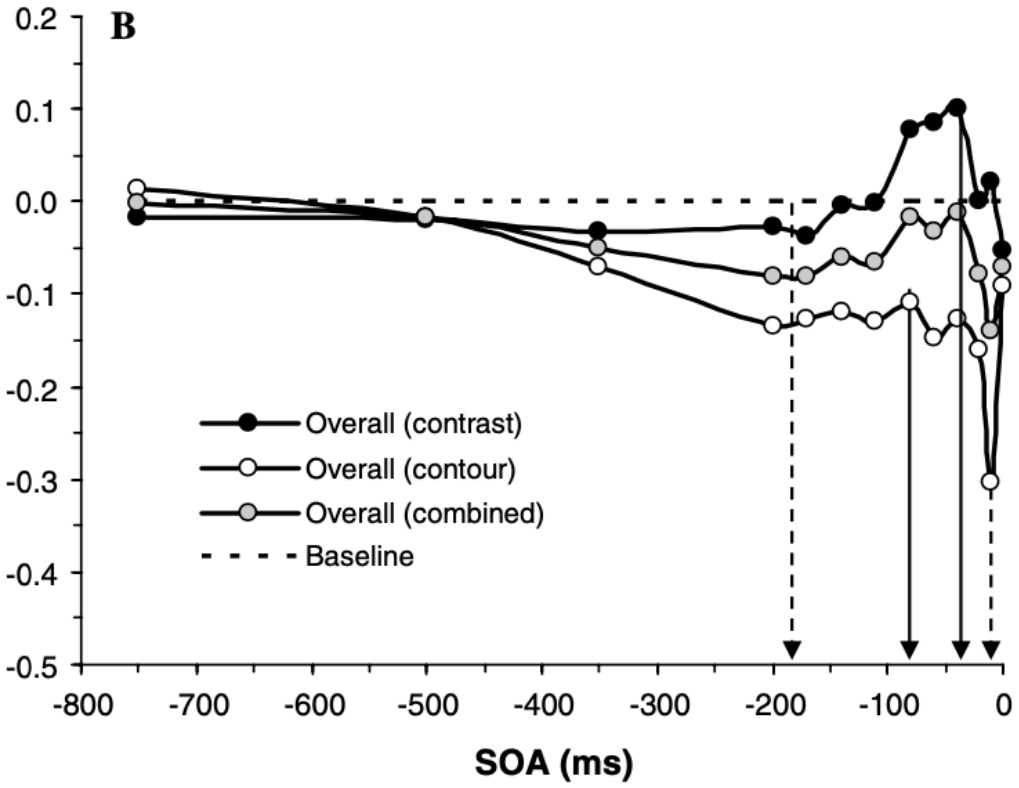

Figure 1.15: Logarithmic perceived visibilities of target during contour discrimination, contrast/brightness matching and combined data. The dashed lines show local minima while solid lines show local maxima. Retrieved from [1]

connections in the cortex. The authors expected to see a shift in the peak facilitation towards the longer SOAs as the spatial separation between target and mask increased. Even though spatial separation decreased the strength of the facilitation peak, no shift was observed in the temporal domain (SOA).

They further investigated the effect of mask contrast polarity in paracontrast by using both brightness judgment and contour discrimination tasks. In Figure 14, the results of the brightness judgment task are presented. When contrast polarity is changed, the peak of the facilitation is shifted from 40 ms SOA to 20 ms SOA, pointing out a significant effect of polarity on facilitation.

Taking into account the three proposed mechanisms underlying paracontrast, they further illustrated that the brief inhibition turns into facilitation at short

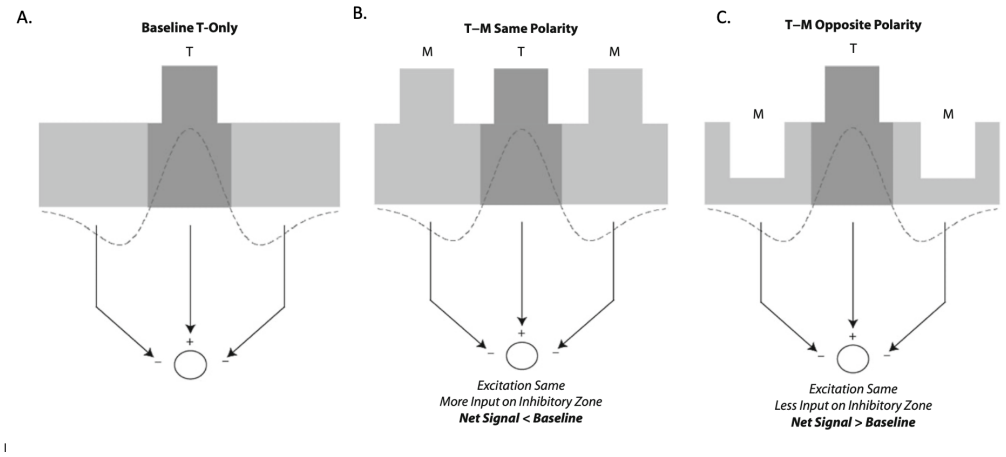

Figure 1.16: Based on the center-on surround-off receptive field profile, the different conditions for target and mask luminance/contrast values are depicted. Retrieved from [2]

SOAs due to a polarity change. Since the brief inhibition is mainly caused by the surround inhibition of the antagonistic center-surround receptive field (i.e., lateral inhibition), they hypothesized that changing the mask luminance to the opposite side may cause a shift in the inhibition effect. Figures 1.16 and 1.17 demonstrates such modulations in the paracontrast masking function. The contrast polarity also influences the masking functions of the contour identification task. In the last experiment of this paper, they checked whether the increased exposure duration of the stimuli is the cause of the increase in the perceived brightness seen in the opposite-polarity condition (Figure 1.14). This effect is mentioned in the literature as a simultaneous brightness contrast effect. Results show that facilitation at low SOA's (around 0-20 ms) in the opposite-contrast polarity is independent of exposure duration.

To sum up, they have two main findings. The first main conclusion indicates that the magnitude of the facilitation decreases as the spatial separation between the mask and target increases or as there is an opposite contrast polarity. The second one is that the contrast polarity has differential effects on brief inhibition and prolonged inhibition. When contrast polarity is opposite between mask and target, brief inhibition becomes facilitation, but prolonged inhibition does not change meaningfully and hence suggests that they have different underlying

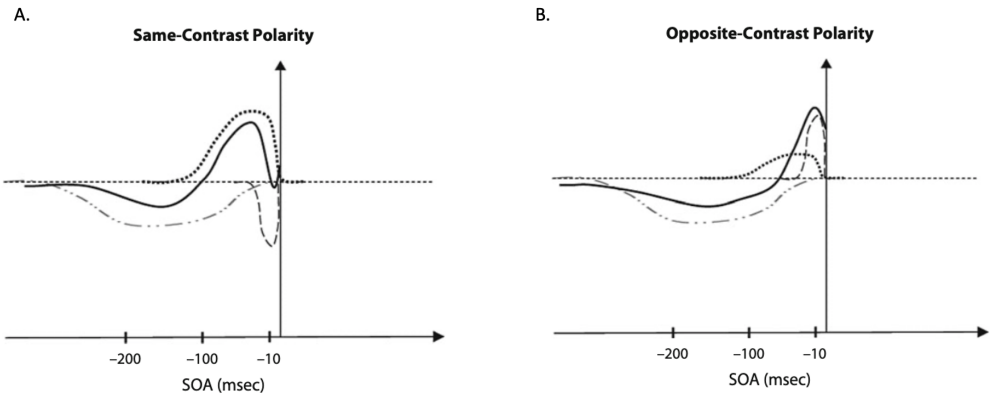

Figure 1.17: A Hypothesis based on the contrast-polarity dependent change in paracontrast masking function and its components. A. Same-Contrast Polarity condition and B. Opposite-Contrast Polarity condition Retrieved from [2]

mechanisms. Furthermore, they rationalized possible neural mechanisms for the components of paracontrast by inferring the results of the contrast polarity experiment. It is implied that brief inhibition is caused by the (inhibition) properties of the center-surround receptive field while the prolonged inhibition is produced by the inhibition/interaction at higher level cortical mechanisms [2].

1.2.4 Recent Theories and Models of Visual Masking

In terms of theoretical models of visual pattern masking, the classification and criteria described by Breitmeyer and Öğmen [8] will be followed throughout the thesis. Several models have been proposed to understand visual pattern masking. Some of them have common main points, while others focus on a completely different aspect. In general, five main groups of models and proposed mechanisms about visual masking can be classified based on the theoretical emphasis of the models that do not mutually exclude each other:

1. Spatiotemporal sequence models,
2. Two-process models,
3. Past-neural network models,

4. Neural-network models adopting overtake and dual-channel activation hypotheses,

5. Object- substitution models.

There are lots of variations under these groups and it is impossible to mention all of them within the context of this specific thesis. Here, only the models related to the specific research questions and experimental design are discussed. Given that "Object-substitution models" are explained in the section of "1.2.1 Common-onset masking", the two models of interest the (i.e., "RECOD" model and the "Perceptual Retouch Model" under "1.2.4.1 Neural-network models adopting overtake and dual-channel activation hypotheses") will be explained and discussed in the following sub-sections.

1.2.4.1 Neural-network models adopting overtake and dual-channel activation hypotheses

While single-channel models take the time relation between stimuli as a rationale for interference between those processes, the dual-channel models put an emphasis on the relative time difference between the processing pathways engaged by common stimulation and propose that the dynamic interaction between these pathways underlie visual masking. These models have a biological basis due to the existence of parallel processing pathways in the visual system (see section 1.1 Human Visual System, Figure 1.3).

1.2.4.1.1 The Perceptual Retouch Model The perceptual retouch (PR) model, introduced by Bachmann (1984), is based on the interactions between two different pathways carrying visual information which are **specific (retico-geniculo-striate)** and **non-specific (retico-reticulo-cortical or thalamo-cortical (as Bachmann [45] called) systems/pathways**. The specific pathways carry visual information from the retina to the visual cortex (V1) passing through LGN. On the other hand, the non-specific pathways also carry visual

information from the retina to cortical areas but stopping by at the reticular systems (i.e., midbrain) not LGN. Furthermore, while contents of the consciousness are controlled by the specific system, awareness's itself is generated by the non-specific system due to the modulatory neurons which are essential for awareness. The model suggests that both of the inputs must converge at the cortical level to generate consciousness. There is a small temporal difference between pathways arriving at the cortex. The specific pathway is a little bit faster than the reticulo-thalamo-cortical non-specific activation. Specific activation for a sensory input arrives at the cortex within 40-100 ms while non-specific modulatory activation arrives at the cortex within 100-150 ms [46]. Additionally, the size of the receptive fields that specific or non-specific pathways hold is different. Non-specific components may gather information from a larger receptive field when compared to specific components [46]. These differences between pathways are the origin of the masking effects.

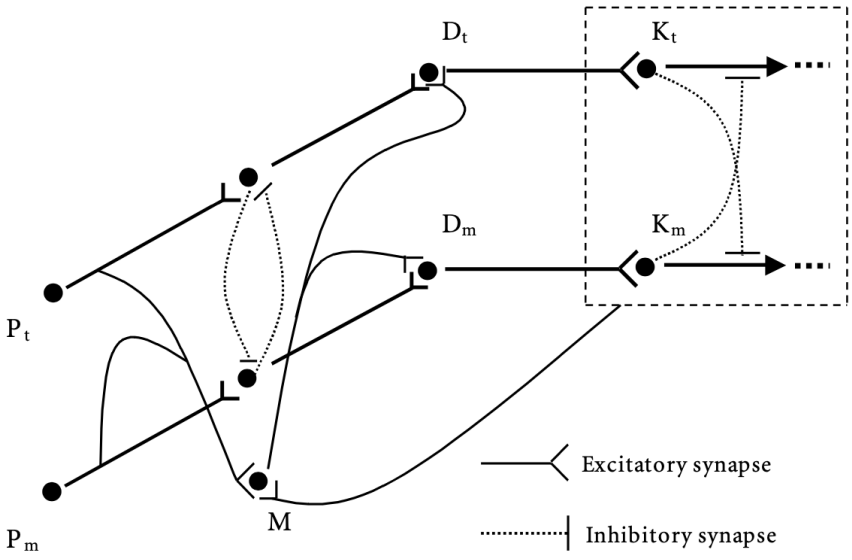

Figure 1.18: Perceptual Retouch model's activation hypothesis for target and mask stimuli. t and m represent target and mask stimuli while P, D and K represent receptors, detector neurons and command neurons, respectively. P, D and K neurons are included in both specific and non-specific pathway. M represents modulatory neurons which is a part of non-specific pathway. Adapted from [8]

In the model, there are also representations for short-latency transient activity and long-latency sustained activity as a part of the specific and non-specific pathway, respectively, which are called phasic and tonic activation. There is also inhibitory interaction within pathways. However, the important reason for masking, according to Perceptual Retouch Model, is not the inhibitory effects or interruptions but is the non-specific facilitatory/modulatory activation caused by the subcortical structures (i.e., thalamic activity) [45]. Facilitatory non-specific activity is generated by modulatory neurons. Figure 1.18 shows how modulatory neurons of the non-specific pathway modulates the activity of the specific pathway. Reticular system activation related to the visual attention mechanisms is also supported by several other studies [47, 48, 49, 50].

In the case of metacontrast, see Figure 1.18 for the representation of the model, both mask and target stimuli generate short-latency specific (SP_t and SP_m) and long-latency non-specific (NSP_t and NSP_m) activation. When these two stimuli are presented too close or too far in respect to time (i.e., SOA equals 0 or is larger than 150 ms), there will be equal activation for D_t and D_m where SP and NSP activations are converged at the cortex. So, K_t and K_m command neurons are activated equally, one of them is not inhibiting the other. Therefore, there will be equal visibility for both target and mask stimuli. However, when there is a moderate time difference (SOA=50 ms) between target and mask, NSP activity generated by the after-coming mask stimulus will arrive at the D location, at the same time as the SP activity generated by the target stimulus arrives. Since there is approximately a 50 ms time difference between SP and NSP activity to reach the cortex, 50 ms SOA between target and mask will cause a temporal convergence between NSP_t and SP_m at the cortical location, D_m. Given that, NSP is a facilitatory activation, D_m will have higher activation than D_t. Similarly, K_m has a larger activation than K_t. Since the activation is not the same, inhibition between K neurons will also not be the same. K_m will more strongly inhibit K_t. Therefore, there will be less activation/visibility for the target for moderate SOA values.

In the case of paracontrast, the PR model has strong assumptions explaining the facilitation component seen under contrast judgment tasks. Similar logic in

the previous paragraph will apply to paracontrast. Since there are two spatiotemporally close stimuli and the mask is the first one and target is the second one (opposite to metacontrast), 50 ms time difference between stimuli will cause an additional excitation on the D neurons of the second stimuli (which is D_t in this case) due to the facilitatory non-specific activation of the first stimulus (NSP_m). In the end, K_t has more excitatory input than K_m which will cause increased visibility for the target stimulus. In this case, the activity of K neurons represents the perceptual salience of the corresponding stimulus.

Bachmann [51] indicates that unconscious processes, perceptual awareness, and attentional effects on performance are controlled by the non-specific systems. PR model is important since it considers the non-stimulus-specific dynamics of the performance in masking research.

1.2.4.1.2 The Retino-Cortical Dynamics (RECOD) Model This model is originally developed by Öğmen [13] to explain how the feedback and feedforward signals and the interaction between them contribute to the dynamics of visual processing. In other words, the initial purpose was to solve the trade-off within the visual system created by the non-linear feedback signals and signals coming from stimulus read-out. Accordingly, the model consists of three phases (Figure 1.19) to reflect the temporal dynamics of visual information processing:

1. Feedforward-dominant phase: The signal generated by the stimulus is transmitted to the cortical areas. This is a strong afferent signal of stimulus read-out.

2. Feedback-dominant phase: At this stage, the afferent signals driven by the stimulus decrease and reach an asymptote at a lower degree, then the feedback (reentrant) signals get stronger and dominant on creating perception.

3. Reset phase: This phase is needed in the case of the stimulus change. Reentrant signals are inhibited fast to allow a new stimulus to make its own afferent signal dominant in the system. Fast transient activity generated by the second/new stimulus inhibits the sustained activity in the system

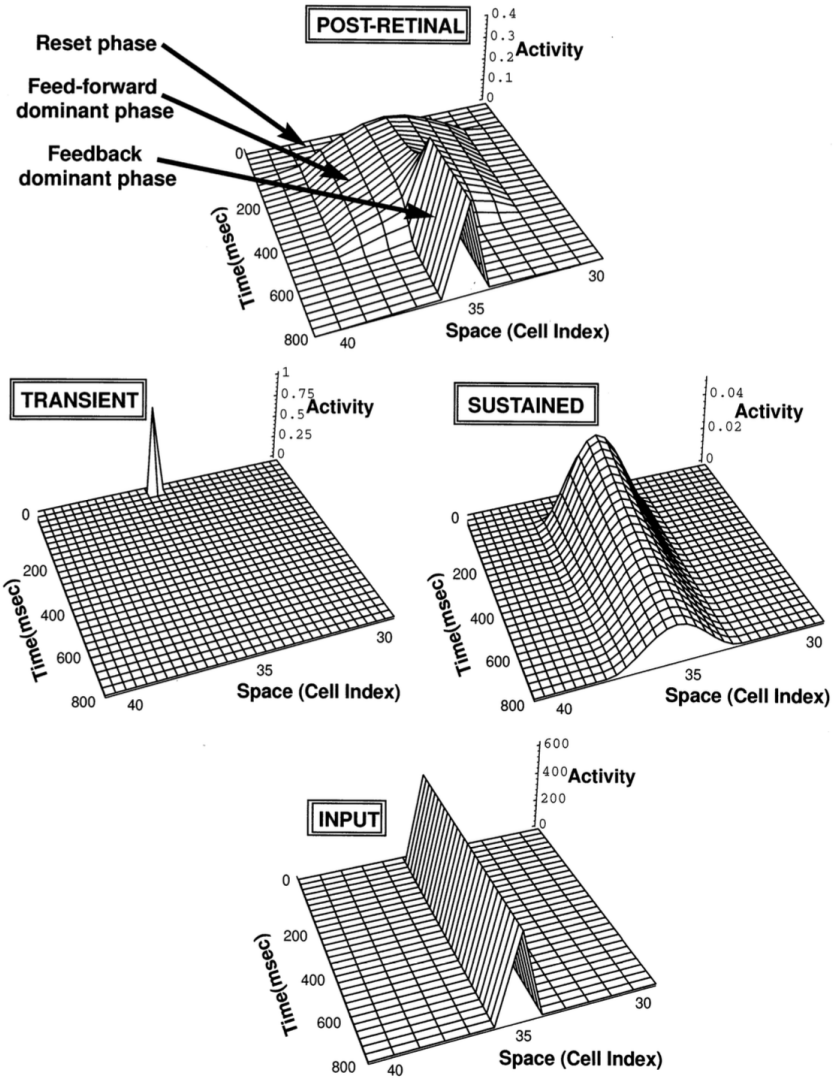

Figure 1.19: The signals at different stages and phases of the RECOD model. The bottom plot shows the input coming from stimuli, entering the system. The plots in the middle row show the transient and sustained activity, respectively, produced by this input. Finally, the upper row shows the post-retinal activity generated by feedforward and feedback loops. The reset phase is also shown in the upper panel. Retrieved from [12].

which is generated by the first stimulus. This transient-on-sustained inter-channel inhibition is the mechanism used to reset the system (see Figure 1.21, arrows between ellipses at top-line)

The model and its predictions are based on the regulation of these phases in real-time. In the model, there are two parallel but complementary pathways that define the phases in the system. The first is a transient signal (i.e., Magno-dominant) that occurs due to the changes in the stimulus and it inhibits the feedback activity and makes the feedforward activity dominant. The second is a relatively slow but sustained signal (i.e., parvo-dominant) activating the feedback loop that continues for a while and then decays to a plateau. The transient activity and its peak define the feedforward phase and the activity decay represents the feedback-phase. Purushothaman et al. [12] summarize the assumptions of the model as follows:

1. Feedback loop is necessary to sharpen the input coming from the sustained channel,
2. Transient signal resets the system from the feedback loop to the feedforward loop,
3. Network dynamics in the post-retinal areas are the result of the aforementioned three phases,
4. Sustained activity must decay to a plateau for the transition from the feedforward phase to the feedback phase.

It is suggested that the activity of the transient channel is sensitive to temporal changes in the stimulus since its inhibitory activation creates the reset phase. The model has been elaborated and has become more comprehensive to account for different aspects of vision [1]. In terms of neuroanatomy, the model is based upon two different types of ganglion cells and their functionally and structurally divergent pathways starting from the retina. As mentioned in the first section, one of these cell types elicits fast but short-lasting activity (transient), while the

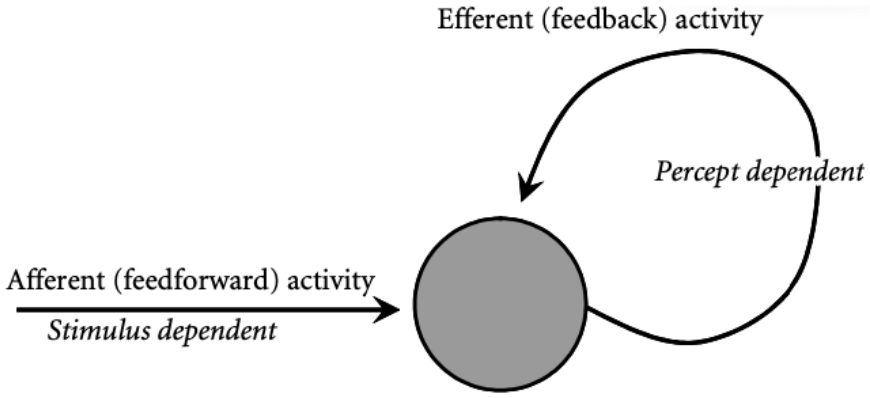

Figure 1.20: Feedforward- and feedback-dominant processes of the RECOD model (Adapted from [8], p.168)

other one has a slow but long-lasting activity (sustained). It is indicated that "the properties of transient and sustain channels in humans and monkeys parallel the properties of magnocellular and parvocellular pathways, respectively" [13]. Thus M-pathway and P-pathway are accepted as neural correlates for afferents in the model. Based on the neurophysiological data, M-pathway provides the main input for the dorsal pathway which is responsible for motion and location estimation. P-pathway provides the main input for the ventral pathway which is specialized for form and color perception. Therefore, in the model, the transient channel refers to the motion-based input while the sustained channel refers to the form-based input. On the other hand, Figure 1.21 shows a brief representation of the system. When necessary, the model may be extended as in Figure 1.23. Figure 1.23 shows different processes driven by the P-pathway (sustained channel). Findings support that contour and surface processing are associated with separate neural mechanisms, P-interblob and P-blob respectively [52]. Accordingly, there are sub-pathways corresponding contour or surface processing under sustained channel (top panel, right ellipses in Figure 1.23). On the other hand, even though both transient and sustained activity carry information for localization it is suggested that the transient activity produces the main input for target localization tasks

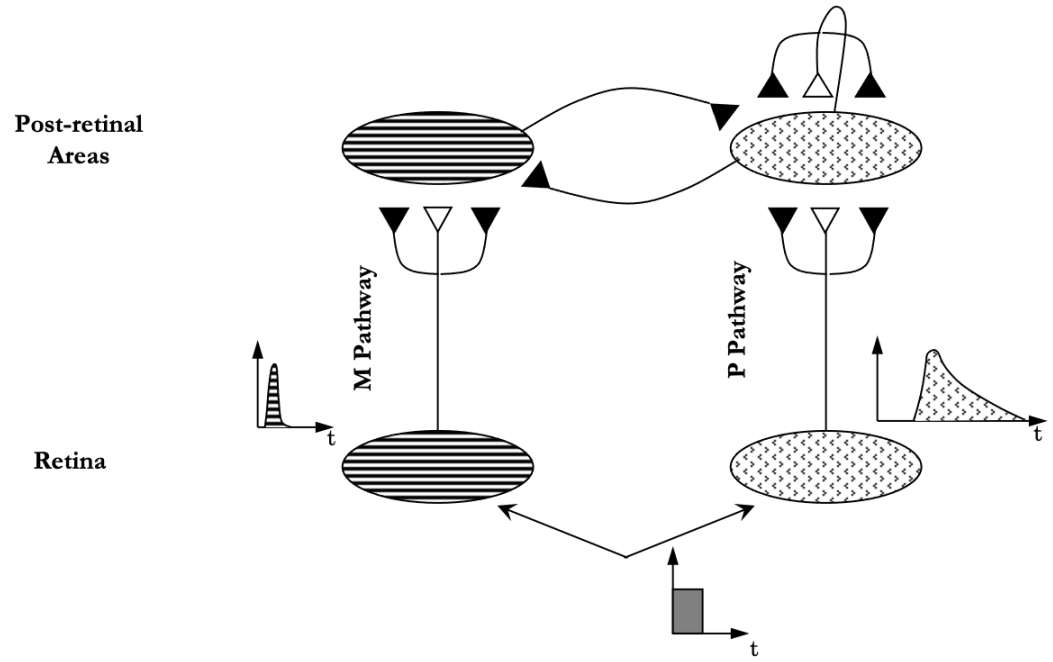

Figure 1.21: An original version of the RECOD model. There are two distinct channels, sustained and transient channels having slow but long-lasting activity and fast but short-lasting activity, respectively. There are inhibitory connections between and within channels. Filled triangles represent inhibitory synapses while open triangles represent excitatory synapses. For simplicity, the recurrent connections at the cortical level are not shown. Retrieved from [13]

when participants are required to answer as fast as possible due to its fast (short-latency) nature [13]. Figure 1.22 shows the model's assumption on change in dominant-channel due to criterion content (transient dominant input in target localization tasks measuring RT). Metacontrast masking does not affect delta-RT and generates a flat curve of RT for changing SOA values. When the mask precedes the target (paracontrast) the SOA modulates the changes of RT, and RT increases as SOA gets closer to zero [13].

In Figure 1.21, the bottom ellipses represent different ganglion cell types. The response types of these cells are also shown in the figure. These afferent pathways, M-pathway and P-pathway follow different routes to the cortex and even pass through different layers of LGN. As mentioned before, these pathways carry information for specified purposes such as motion or color perception. Mounting evidence suggests that these pathways interact at the cortical level. The model

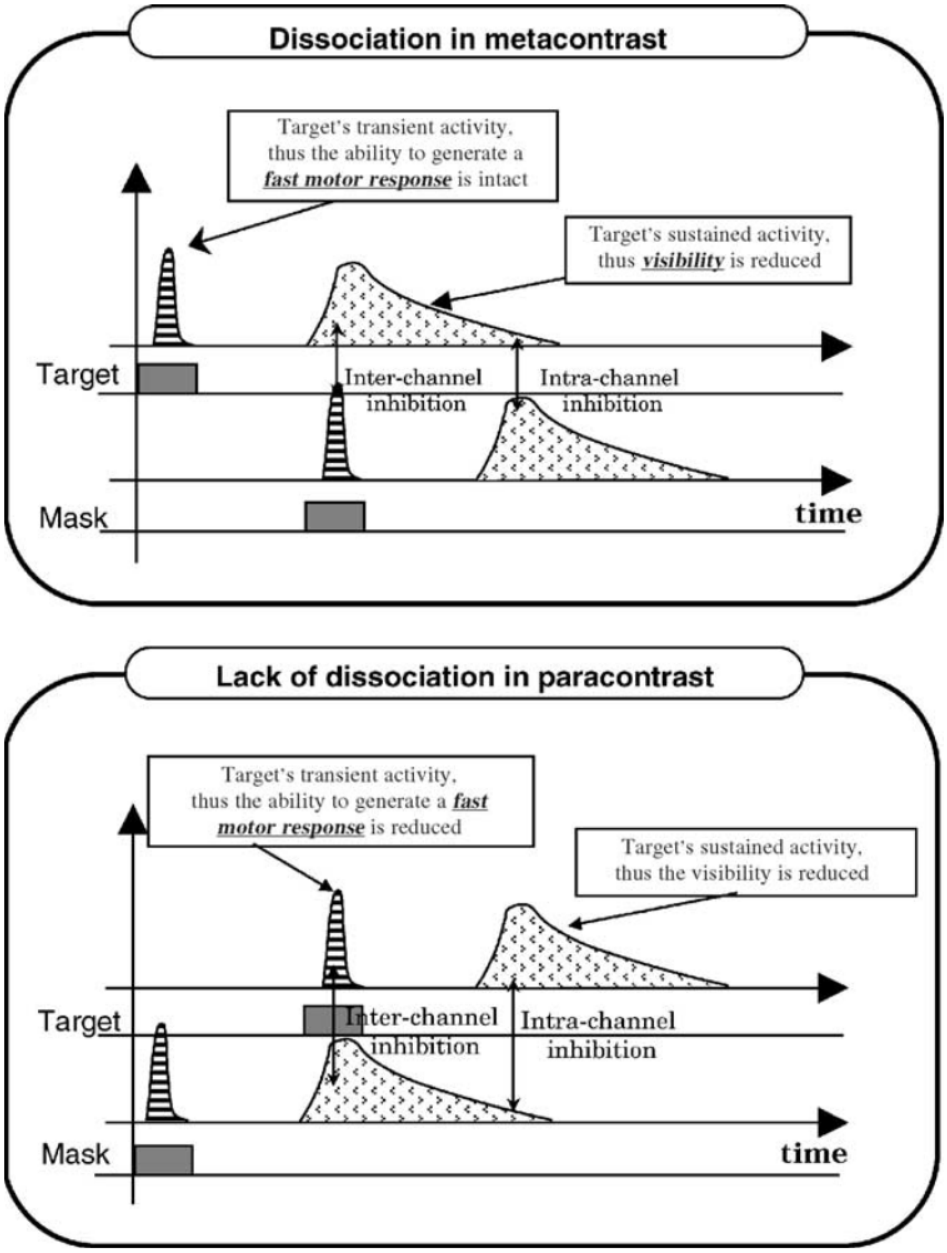

Figure 1.22: Predictions of RECOD model on target visibility and reaction times generated by metacontrast (top) and paracontrast (bottom). Retrieved from [13]

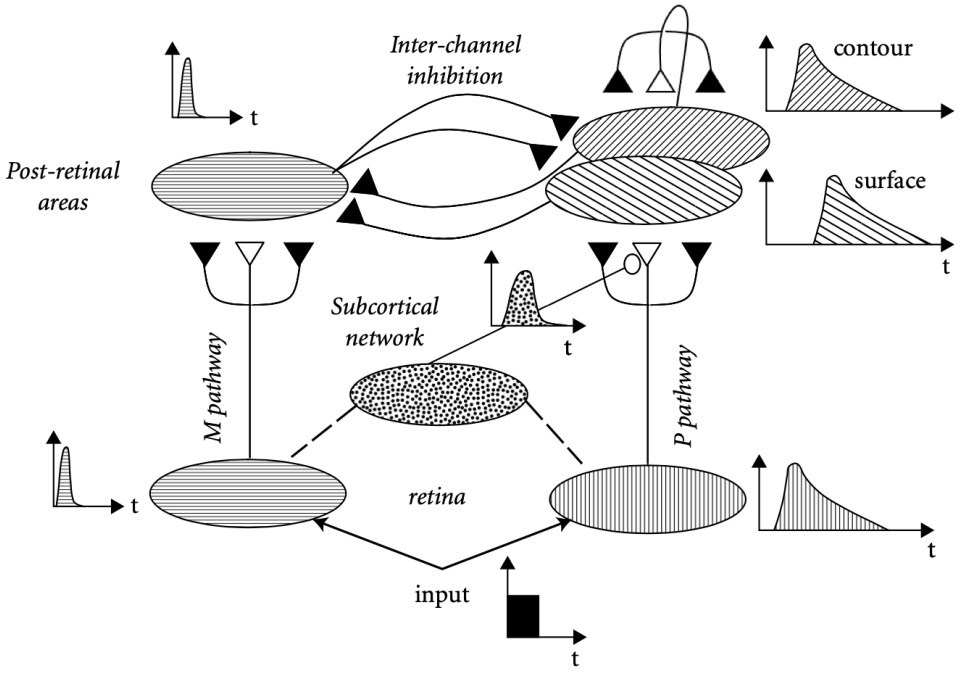

Figure 1.23: Elaborated version of the RECOD model. As in the PR model, a subcortical network having multiple synaptic interactions to modulate the input in the main streams was added to the model. Also, sustained channel wasdivided into two sub-pathways at the cortical level to have distinct contour and surface processing. Retrieved from [8], p.175.

approximates this interaction/inhibition between pathways with inter-channel inhibition (Figure 1.21, arrows between top ellipses). Also, the model postulates an inhibitory interaction within channels/pathways which is named intra-channel inhibition. These two types of inhibition have been proposed to underlie metacontrast and paracontrast masking.

As seen in Figure 1.23, a subcortical network is added to the model [1]. As in the PR model, the subcortical network corresponds to a lumped representation of subcortical areas which modulates and enhances the activity in cortical areas. There are also feedback (i.e., recurrent) connections at the cortical level, but they are not shown to avoid complexity. Another modification of the model by Breitmeyer et al. [1] is the differentiation of the contour and surface processes. Even though both of them take input from sustained channels, the surface information reaches later than the contour information which causes differentiation of

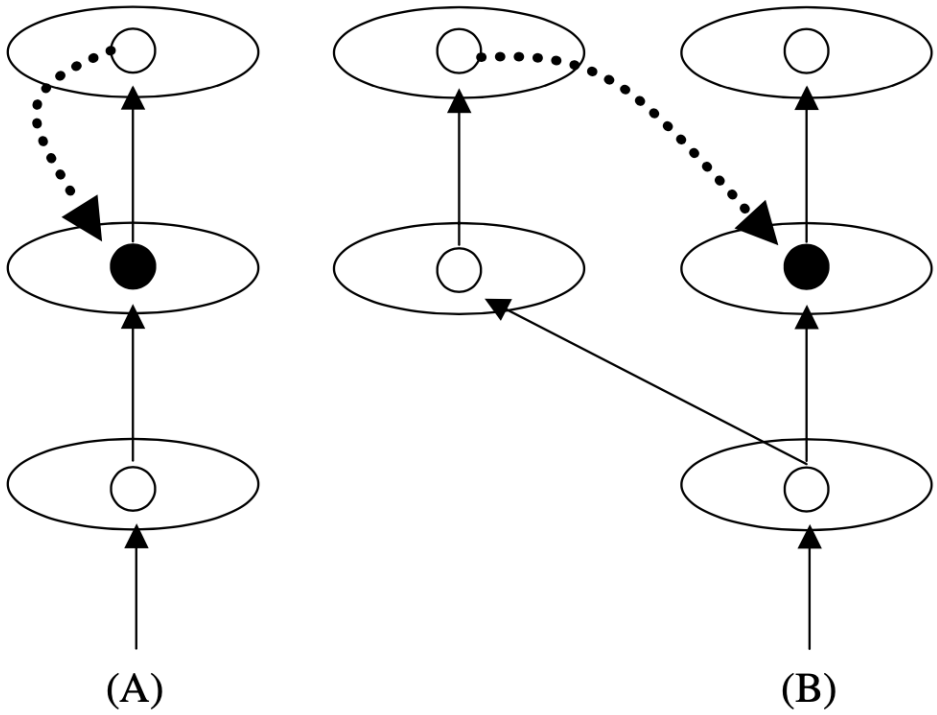

Figure 1.24: Dashed lines represent anatomical efferent signals producing cortical intra-channel inhibition causing prolonged inhibition in paracontrast. (A) shows the possibility of these signals are functionally feedback while (B) shows that these signals are functionally feedforward signals. Retrieved from [13]

masking functions between the perceptual tasks (brightness matching vs. contour discrimination).

The predictions of the RECOD model for the underlying reasons of masking effect (decreasing in target's visibility) are based on the intra-channel and inter-channel inhibitions for paracontrast and metacontrast, respectively.

Each stimulus generates activity in both fast-transient and slow-sustained channels. At the cortical level of the sustained channel, contour and brightness information are processed in different/distinct subpopulations. The surface (brightness) process is slower than the contour process, even though the contour process still generates slow and sustained activity (Figure 1.23). The RECOD model suggests that transient activity of the preceding mask interacts with the

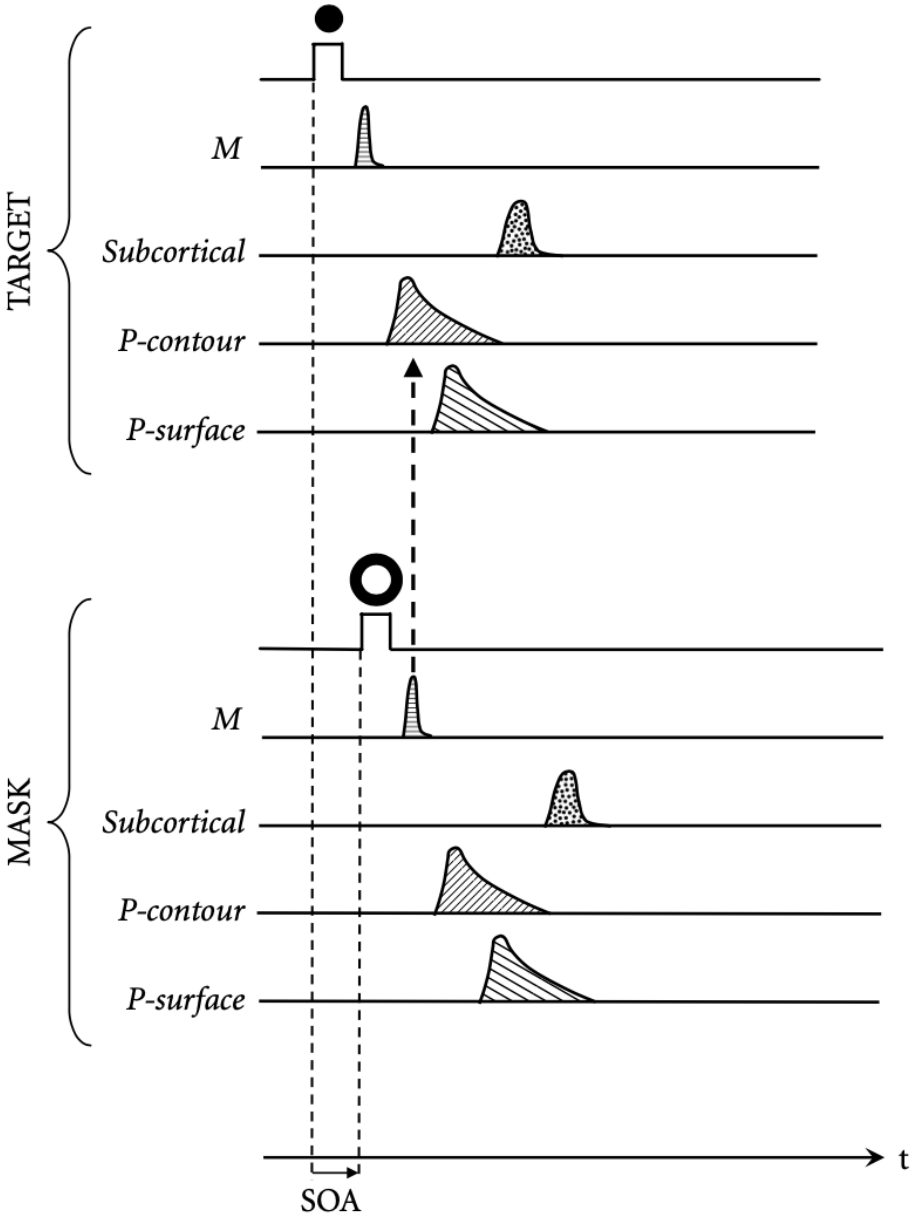

Figure 1.25: RECOD model explanation on metacontrast masking. Temporal difference between contour and brightness process causes a shift in the optimal SOA of Type-B metacontrast masking function, although the underlying mechanism is the same (interchannel inhibition is causing the metacontrast effect). Retrieved from [8], p.176

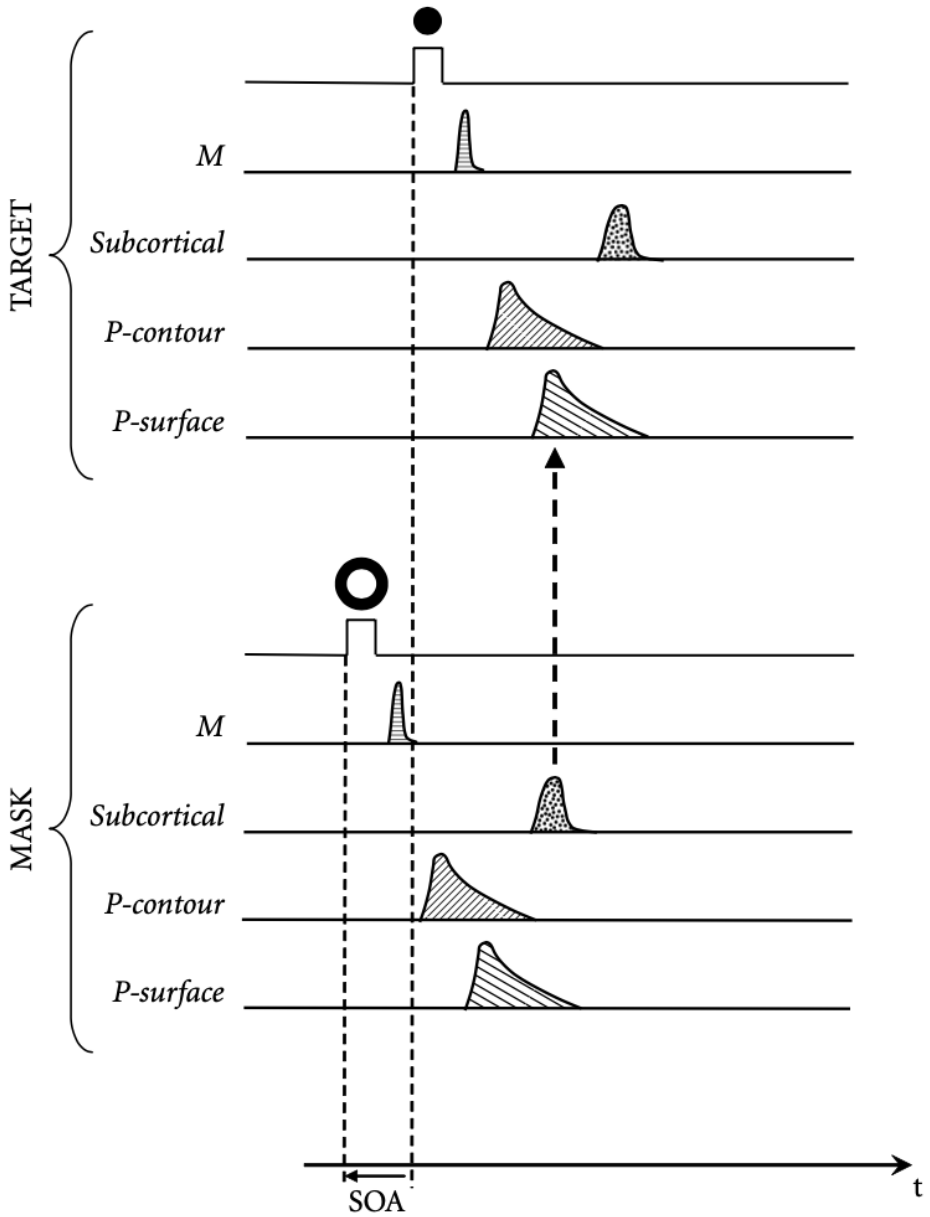

Figure 1.26: Predictions of RECOD model on paracontrast facilitation. Retrieved from [8], p.178

sustained activity of the target, in metacontrast. This inter-channel inhibition between transient and sustained channels (transient-on-sustained inhibition) forms a Type-B metacontrast masking effect decreasing the target visibility by decreasing the target-based sustained activity. As Figure 1.12 shows, the Type-B metacontrast masking function has a typical U-shape which reflects maximum masking effect at intermediate SOAs while smaller-or-non masking effect is observed as SOA approaches 0 ms or 500 ms. Also, a previous study shows that contour discrimination and brightness judgment tasks produce U-shape function, but their peak is shifting. Metacontrast function for the contour discrimination task peaks at 10-20 ms while for the brightness judgement task the peak is at 40 ms [1]. The expectation of the model fits with these results since contour processing is slightly faster than surface processing, it interacts with the transient activity of the mask earlier. Figure 1.25 clearly depicts this explanation. RECOD model explains the Type-B (non-monotonic) masking function well by demonstrating the transient-on-sustained inhibition on target [13]. Authors [13] further denoted that the response criterion of the participants determines the dominant channel (transient or sustained) and therefore determines the type of masking function, being monotonic or non-monotonic.

As mentioned before, there are two inhibitory and one facilitatory component in a typical Type-B paracontrast masking function, see Figure 1.13. Since the excitatory center activation is 10-30 ms faster than the inhibitory surround activation in a classical center-surround receptive field when the mask precedes the target 10-30 ms the inhibition is optimum due to this intrachannel inhibitory interaction. This explanation of the RECOD model fits with the brief inhibition. For the case of prolonged inhibition, RECOD model suggests an explanation consisting of the intrachannel inhibition at the cortical level. In terms of the underlying mechanism of cortical intra-channel inhibition producing prolonged inhibition of paracontrast, it is hypothesized that anatomically efferent signals are involved. These anatomically efferent signals may be functionally feedforward or functionally feedback signals, see Figure 24 [13]. However, the exact mechanism is not known yet [13].

Figure 1.22 shows sustained, and transient activities produced by the target

and the mask, as well as inter-channel and intra-channel inhibition. As indicated in the text in Figure 1.22, the inter-channel inhibition is the reason for increased reaction time observed in studies of paracontrast [13]. Intra-channel inhibition between sustained input of mask and sustained input of target is the reason for the decreased visibility of the target.

It is indicated that facilitatory subcortical activity is 50 ms slower than the cortical activity [1]. So, if the first stimulus (mask) is presented 50-60 ms earlier than the second (target), the subcortical activity of the first stimulus will optimally enhance the cortical activity of the second one. This matches with the paracontrast facilitation findings. Figure 1.26 shows this relationship. In addition, researchers find that paracontrast facilitation is observed when the task is surface(brightness) judgment rather than the contour judgment. This finding is also parallel with the expectations of the RECOD model on paracontrast facilitation, see Figure 1.26 (the subcortical activity of the mask mostly encounters with the surface-based sustained input of the target, not with the contour-based input.)

1.2.5 Attention and Memory

1.2.5.1 The Three-Store Model of Information Processing

There are several memory models about how sensory information is processed in the brain. The three-store model proposed by Atkinson and Shiffrin [14] is a widely accepted traditional model of memory which explains how distinct components of the memory process the sensory information. The three-store model proposes that there are three physically distinct memory components/stores in the brain that keep and process coming information, sequentially. These are the sensory store that stores high amounts of information for a short time, the short-term store which is capable of storing relatively limited information for a long time as compared to the sensory store and the long-term store with a large capacity for both amounts of information and duration of storage. For the sensory store,

Atkinson Shiffrin [14] originally used the term "sensory register" which refers to the initiation role of this component through the system. Also, although the model defines these components as "stores" and differentiates them from memory, the common recent perspective uses the term "memory" rather than "store".

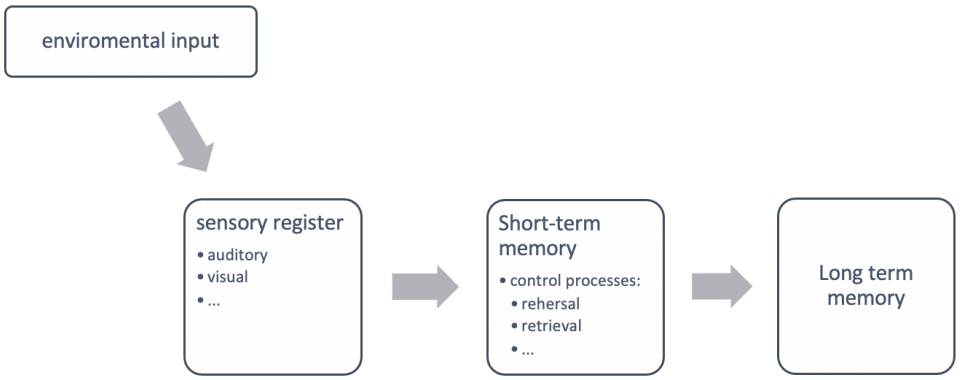

Figure 1.27: Schematic representation for Three-Store Model of Information Processing by Atkinson and Shiffrin [14]

As one can see in Figure 1.27, the incoming information enters the system through the sensory store. A distinct storage part of the sensory store which is specialized for visual input is named the iconic store (i.e., sensory register) discovered by Sperling [53]. Iconic memory also has two components: visible and informational persistence. As widely used in the literature of cognitive psychology, an "icon" refers to a unit of an object as it is represented in the memory. Supported by both Sperling's [53] and others' work, the information in the iconic memory decays fast. Therefore, after entering this system through iconic memory, the visual information is either sent to another memory location [14] or erased [54]. It is also suggested that this "erasing" may seem as an example of metacontrast masking [55]. The second stage of the system is short-term memory or short-term store as Atkinson and Shiffrin defined. Short-term memory which passively stores the information is slightly different from working memory which actively manipulates the information [56]. It has the advantage to hold memories (icons) longer than sensory (iconic) memory in terms of storage duration;

although it has limited capacity in terms of the number of items that it can store at a time. In general, accumulating evidence indicates that the storage capacity of the short-term memory is seven items with plus or minus 2 [57]. The time limit of this storage is up to 20 to 30 seconds [56]. It has been suggested that short-term memory is the level where the information is available consciously [58]. Even though verbal stimuli are used in most studies on the capacity of short-term memory, short-term memory is also investigated in terms of keeping visual information. Visual short-term memory is accepted to have a capacity for 4 items rather than 7 as originally claimed by Cowan [59].

Findings expressing that visual masking can interfere with the iconic memory but cannot interfere with the VSTM also supports the distinction between these components of the memory. This property of the visual mask makes it an efficient tool for visual memory studies. As suggested before [3], it makes it possible to study VSTM in isolation since the mask suppresses the representation of the stimuli in iconic memory.

On a daily routine, we, generally, use the information in the short-term memory, and sometimes, use the information in the long-term memory that is consolidated and long-lasting. As long as we attend, the information in the short-term memory is kept, but when attention is dissolved, the information in the short-term memory is lost unless it is transferred to the long-term memory. Long-term memory can hold a large amount of information for a long time. Bahrick [60] proposes that the capacity of long-term memory is infinite. Even too old but solid memories are being kept after years and this phenomenon is named as permastore by researchers. However, some of the information cannot be transferred to long-term memory and are either erased during the selection process from sensory to iconic memory or cannot be selected and transferred from short-term to long-term memory and fade away. When a unit of information arrives in long-term memory after all these selections and erasing processes, this information is kept for a long period and can be used any time being recalled by the working memory.

To sum up, iconic memory is a part of sensory memory that is responsible for

visual information. After the visual information is taken to the system through iconic memory, it is either selected or transferred to the visual-short term memory to be processed at a more advanced level or erased. As mentioned in the following sections of this thesis, this selection process from iconic to visual short-term memory is suggested to be controlled by both attention [15] and visual masking [3].

Visual masking cannot interfere with the information in the visual short-term memory while research suggests that it is the opposite for iconic memory[3].As indicated by Agaoglu [30], this feature of visual masking helps to study VSTM alone by suppressing the contents of iconic memory through a visual masking paradigm. As in this example, visual masking is frequently used as a tool to study the visual system.

1.2.5.2 Spatial Attention

As described in the previous sections, in daily life, constantly changing 2-dimensional images are captured by the retina and through the visual system we perceive clear scenes with correct proportional sizes even during eye movements. At each moment, the visual system processes a different scene/image that falls into the retina and creates visual perception using that consistent information. "Leaky hourglass" analogy describes visual information processing as in Figure 1.28. The continuous information coming to the system is first transferred, after encoding by the visual system, to iconic (sensory) memory. Iconic memory keeps the information only for a few hundred milliseconds which refers to the "leak" of the system. Then, the visual information, stored by the sensory memory, is selected and transferred into visual short-term memory (VSTM) that has a higher limit of keeping information but a small capacity in terms of the number of items. This selection process is led by attention, as the hourglass analogy shows [15].

Attention is described as having a limited capacity and selective nature, even in the earliest writings [61]. Besides its selective nature, in Leaky Hourglass Model, Load Theory of Attentional Selection suggests that this selection is based on the

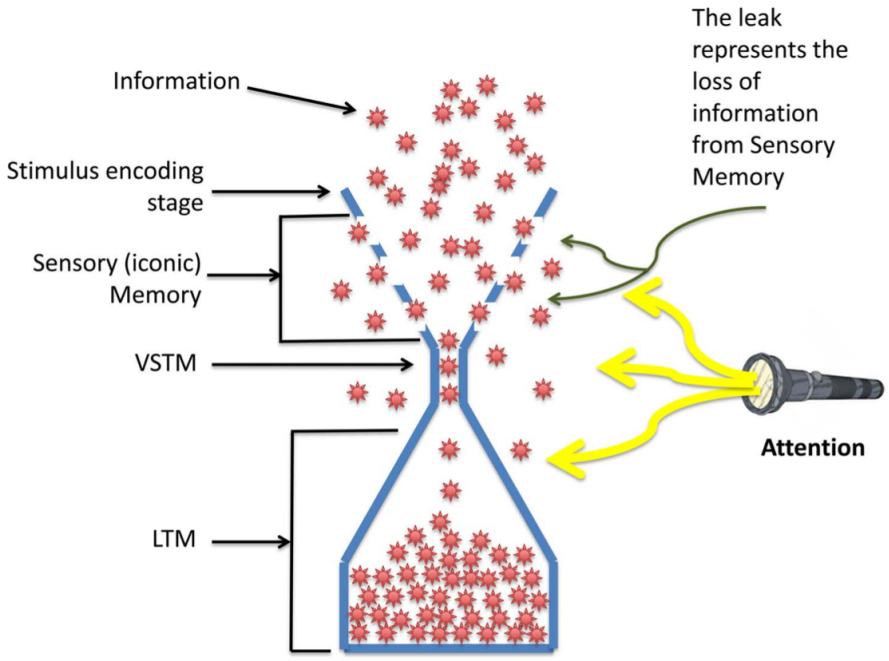

Figure 1.28: The Leaky-Hourglass Analogy. It describes the visual information processing through memory systems. Information from the stimulus is encoded and sensory (iconic) memory can hold almost all of the information of the entire visual field, since it has wide capacity. However, as shown, it leaks as time goes. It can hold information only for a small time. Then, some of the information is chosen and transmitted to the Visual Short-Term Memory. This selection is based on the importance (under the guidance of attention). Retrieved from [15]

relevant and irrelevant information, and hence its resources are goal-directed. Attention also has a limited capacity; thus, a selection should be made. Load theory indicates that firstly the target stimulus gets its necessary attention from a limited capacity resource, then the rest of the resource is shared by other stimuli (distractors). Therefore, it depends on the usage of the attentional resources by the target stimulus that how many resources will be there for the unattended stimuli [62]. Based on this theoretical perspective, set-size is used to control attentional load in a task [3].

1.3 Specific Aims

Although attention controls the information flow by enhancing it while visual masking controls the information transformation by inhibiting, they are both effective on the same processes. Thus, since both attention and visual masking control the information flow from iconic memory to VSTM, there is an ongoing debate on whether these processes work independently or not. Even though *Object Substitution Theory* claims that there is an interaction between these processes, recent studies suggest that those findings are based on artificial/genuine interactions due to ceiling/floor effects of masking [33]. An aforementioned study by Agaoglu et al. [3] further investigated the existence of an interaction between metacontrast masking and attention avoiding ceiling and floor effects and found no evidence of such interaction.

In terms of design and conceptual framework, this thesis originated from the experimental paradigm used by Agaoglu et al. [3]. We wanted to identify the relationship between attention and the proposed mechanisms underlying paracontrast masking using a similar design. In their study, they [3] used bars with random slopes on an imaginary circle around a center (fixation) point and a ring-shape non-overlapping mask was presented after the target. The task was to decide the angle of the target bar's slope and adjust the slope of the randomly tilted response bar presented at the center at the end of each trial. In this metacontrast paradigm, there was a confounding factor that the authors mentioned in their follow-up study [10].

Although the masking theories cover both forward and backward masking, the literature have mainly focused on the backward masking paradigm. One possible reason for that is the intrinsically interesting nature of the backward masking which refers to the inhibition of an after-coming target. In contrast, paracontrast did not take attention since mask comes firstly. However, Type-B paracontrast function shows that this is not a basic interaction between mask and after-coming mask. If it would be the case, the masking function must be a Type-A function. But in Type-B paracontrast, there is a non-linear relationship between SOA and

masking and there are several components which cannot be explained by the basic notions such as temporal order of stimuli. The other possible reason of this focus is the relatively simpler function of the metacontrast which creates U-shape function and mathematically it refers to a second order function. On the other hand, paracontrast creates more complicated, mathematically, function having more than one extrema. Hence, there is a gap in the literature on paracontrast research and paracontrast masking needs to be studied extensively in further studies.

Thus, in this thesis, the interaction between attention and masking was studied by focusing on the paracontrast/forward masking. Based on the findings in the literature, attention is expected to modulate different components of the paracontrast masking differentially. First of all, the facilitation component is expected to be found in the brightness judgment task while inhibition components are expected to appear under the contour judgment task. Since the facilitation component has been suggested to be mainly mediated by the sub-cortical structure and non-specific pathways, it is likely to observe a modulation of attention in the facilitation component. Furthermore, as the RECOD model claims, prolonged inhibition and brief inhibition is caused by separate underlying intra-channel inhibition mechanisms and thus, these components may be affected by the attentional manipulation distinctively. In all cases, the prospective findings will contribute to the literature since it is an open question of whether attention interacts with visual masking or not. Additionally, paracontrast masking is less studied due to its complexity. Therefore, additional information on the nature of paracontrast masking is also important for masking research. Even though recent metacontrast studies suggest that visual masking does not interact with attention [3, 10, 33], we expect to see a modulatory effect of attention on paracontrast masking which is not conflicting with these studies since metacontrast and paracontrast masking have been proposed to have engage different neural mechanisms. The direction of the modulation will provide further information about the nature of such modulations and interactions.

Chapter 2

Attentional Effect on Brief and Prolonged Inhibition of Paracontrast Masking (Experiment 1)

This chapter is dedicated to the first experiment of my thesis project which aims to reveal the possible interaction between attention and paracontrast masking via a contour discrimination task. As mentioned in Chapter 1, having scientific knowledge on this interaction is important since it will support or reject theoretical expectations and give specific information on the structural and functional features of both memory components and visual processing. As a former study [1] declared, inhibitory and facilitatory components of the paracontrast masking function are revealed by different tasks. Criterion content is also effective on the appearance of these task-based components. Based on the results of the aforementioned study, we expected to see inhibitory components (both brief inhibition and prolonged inhibition) but not the facilitatory component at the current experimental design which uses a contour judgement task [1].

Furthermore, the RECOD model suggests that brief inhibition is caused by the

intra-channel inhibition of sustained channel (P-pathway). Also, it is indicated that center-surround antagonistic relation of receptive fields in retina supports this early inhibitory interaction [1]. On the other hand, prolonged inhibition is suggested to be produced by the late intra-channel inhibitory interaction of sustained-contour channel. Neurologically, this refers to cortical level interactions within P-pathway.

In this experiment, we examined whether attention modulates the inhibitory paracontrast components and if it does, how these inhibitory mechanisms at different hierarchical levels are modulated by attention.

2.1 Method

2.1.1 Participants and Apparatus

Eight observers (age range 18-26) took part in this experiment. All the participants had normal or corrected-to-normal vision. None of them had a history of neurological disorders. Informed consent was signed, and a pre-screening form was filled by each participant prior to the experiment. All procedures were in accordance with the Declaration of Helsinki (World Medical Association, 2013) and approved by the local ethics committee at the Bilkent University.

Stimulus presentation, experimental paradigm, and data acquisition were controlled by MATLAB (The MathWorks, Natick, MA) with the Psychtoolbox [63, 64]. A 20-in. CRT monitor with 1280 x 1024 resolution and 100 Hz refresh rate was used to display visual stimuli. A photometer (SpectroCAL, Cambridge Research Systems, Rochester, Kent, UK) was used for luminance calibration and gamma correction of the display. There was approximately a 57 cm distance between the participants and the screen. The left and right arrow keys of a keyboard were used to acquire behavioral responses from participants. The experimental sessions were performed in a silent and dark room.

2.1.2 Stimuli and Experimental Design

The origin of the experimental design was the study of Agaoglu et al. [3]. We adopted this design by using the previous contour discrimination tasks of paracontrast masking [1, 2]. The specific stimulus parameters and other fine changes in the experimental design were carefully adjusted through pilot behavioral studies. The visual stimulation is described in Figure 2.1.

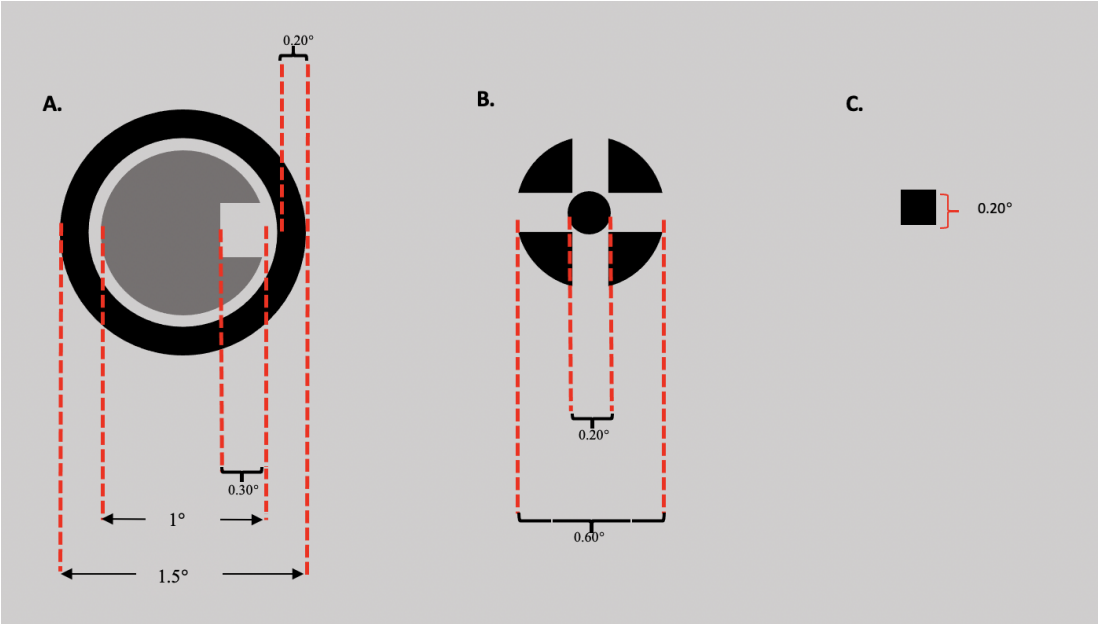

Figure 2.1: **A.**The target and mask stimuli. The target (or distractor) is placed inside the mask ring. **B.** The fixation point which was a combination of bull's eye and cross hair). **C.** The baseline cue .

A central fixation point on a gray background (48.3 cd/m^2) was present throughout an experimental session. As the shape of the fixation point, a combination of bull's eye and cross hair was used as it was found to be one of the best options to minimize eye movements [65]. Minimizing eye-movements/saccades has a crucial value in an attention study, because a previous recording study found that preparation of saccadic eye-movements can modulate the activity in the visual cortex (e.g., [66]). Therefore, possible large saccadic eye movements of a participant could create an important confound in terms of specific experimental questions of the current thesis. The target and distractors were light gray (33.3 cd/m^2) while the mask and cue for baseline conditions were dark gray (1.3

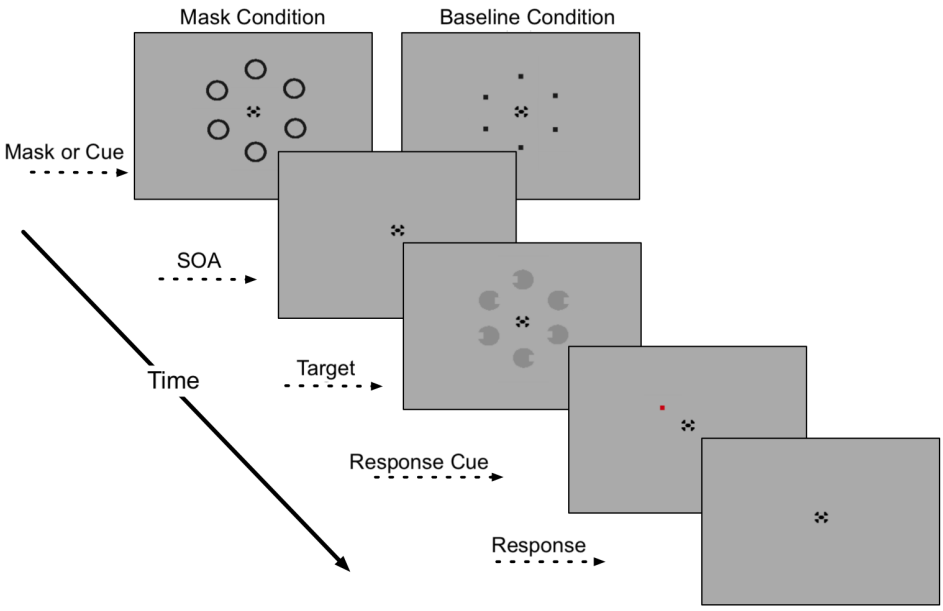

Figure 2.2: The schematic representation and timeline of Experiment 1, for set-size 6 condition.

cd/m^2). All visual stimulation was darker than the background. Figure 2.1 shows the shape and size of the stimuli. The target and mask stimuli did not overlap in space. Target is a filled-round stimulus (with 1° diameter) with a notch (0.30° sized square) either on its right or left. The mask was a ring-shaped stimulus surrounding the target (inner and outer diameters are 1.1° and 1.5°). The target and mask separation was 0.05°. The response cue was identical to the cue used in the baseline condition but it was red.

The design included set-size, mask-type, and SOA as the main experimental factors (2 set-size x 2 mask type x 11 SOAs). There were two set-size conditions, having either two or six stimuli, to manipulate the attentional load in the spatial domain (Figure 2.2 and Figure 2.3). The mask stimulation was either an annulus disk or a baseline cue. Moreover, 11 SOA conditions were used: 0, 10, 20, 40, 60, 80; 110, 140, 170, 200 and 350 ms. All the experimental conditions were shuffled and presented randomly throughout the experimental session. Firstly, each participant attended two training sessions. One of them consisted of only baseline cue trials with 20 repetitions from each SOA condition and the other

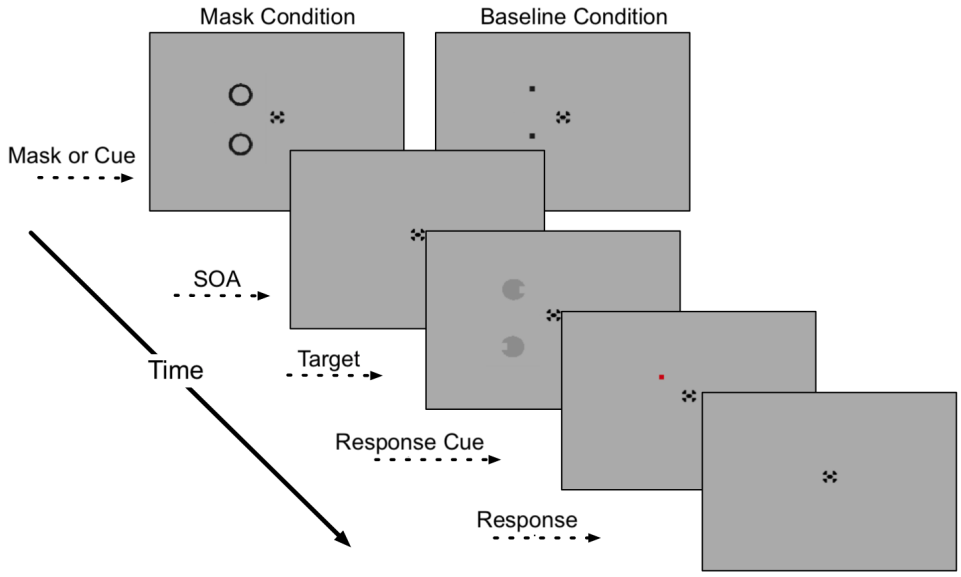

Figure 2.3: The schematic representation and timeline of Experiment 1, for set-size 2 condition.

training session included both mask annulus and cue trials of varying SOAs with 15 repetitions. With these training and practice sessions, we aimed to reduce the within-subject variability caused by the incompetency on the task. Also, it helped us to eliminate subjects who were not able to meet our objective criteria. After participants accomplished practice sessions, they completed five experimental sessions including 20-repetition of each condition, total of 4400 trials (100 trials per condition). Complete design of a possible trial in a session is presented in the Figure 3 and 2 (for set-size 2 and 6, respectively). A trial may be one of the 44 possible condition (2 set-size x 2 mask types x 11 SOAs). After all trials of a session were determined, the presentation order of the trials was randomized. An experimental session with 20 trials for each condition lasted approximately 40 minutes.

At the beginning of each trial, a blank screen was presented for a variable time-interval (500-1000 ms). Afterward, if it was a mask trial, two (six) mask rings were presented for 20 ms at the locations of the target and distractor(s), on an imaginary circle with 4° diameter centered to the fixation point. For the baseline

cue trials, little black squares were presented for 20 ms referring to the locations of following stimuli (i.e., target and distractor(s)), on an imaginary circle with 2° diameter centered to the fixation point. After the presentation of the mask or cue, a blank screen was displayed for a specified time according to the defined SOA of that specific trial. The target screen was presented for 20 ms at the end of the SOA. The target screen consisted of two (or six) filled-round stimuli with a notch on their left or right side which were aligned on an imaginary circle with 4° diameter centered to the fixation point. Only one stimulus on the screen was the target, the others acted as distractors. Each stimulus in the target screen had the same size, shape and color but they differed in terms of the side that the notch appeared. The notches were located to the left or the right sides of each stimulus randomly. 100 ms after the target screen disappeared, a small red square (having the same size and shape as the baseline cue, but its color is red) was presented as a response cue on an imaginary circle with 1.2° diameter centered to the fixation point referring to the location of the target stimulus. The response-cue stayed on for 150 ms and informed the participants about which one was the target. After the response-cue disappeared, a blank screen was presented and the participants were expected to decide the side of the notch for the target stimulus, using the right or left arrow keys (referring to the side of the notch for target stimulus).

For the target, the round stimulus with a notch was chosen rather than a tilted bar since our pilot studies (and observations) showed that this type of target stimulus was ineffective to observe inhibitory masking effect in paracontrast. Compared to metacontrast, the effective range of target-mask spatial separation is more limited in paracontrast [8]. Thus, since a bar with 1 length and 0.1° width in a ring with 1.1° diameter (as a target-mask pair used in Agaoglu et al.,2016) causes relatively a larger separation between target and mask, it may reduce the effectiveness of the mask in paracontrast.

2.2 Data Analysis

After each session, the percent correct values for each experimental condition were computed by dividing the total number of correct responses by the total number of trials (i.e., 20 trials per condition). Therefore, after a session, we had one quantitative value for each of the 44 experimental conditions. To control floor and ceiling effects, we used the following pre-determined criteria:

1. The percentage for correct values of each experimental session was calculated right after the session and should be higher than 50% which is a chance-level to eliminate the floor effect.

2. To eliminate the possible ceiling effect, the percent correct values of a participant should not be around 100%.

After each condition was quantified for a specific session, the masking effect was calculated for each SOA and set-size by normalizing each annulus mask condition with the corresponding baseline cue condition. Normalize values were calculated by dividing masking data by corresponding baseline data. For each session of every participant, the normalized values were used to quantify the masking effect in each SOA and set-size condition. This session-based normalization also restricted the contribution of any confounding factors such as daily-changes in raw performance values. The normalized values were used to calculate the average values of a specific participant and group/population average. A two-way repeated measures analysis of variance (ANOVA) with SOA and set-size as factors was performed on the normalized and averaged values. Additional follow-up paired t-tests were also carried out to compare set-size conditions by using the data in the specific range of brief and prolonged inhibitions.

2.3 Results and Discussion

Figure 2.4.A shows the raw percent correct values for all conditions of set-size 2 trials. The continuous line with filled circles, and dotted-line with hollow circles represent the data for annulus mask and baseline-cue conditions as a function of SOA, respectively. Using the same conventions, the data for set-size 6 is presented in Figure 2.4.B. Since paracontrast is a forward masking paradigm, the negative SOA values correspond to the onset timing with a preceding mask/cue and the target. There were two possible choices (left vs. right) that the participants could respond to at the end of a trial, and hence 50% correspond to the chance-level.

As shown in Figure 2.4.A the percentage values as a function of SOA are almost flat for the baseline-cue conditions. This is in line with the original expectation since the cue conditions were optimized as a baseline condition to control confounding factors and not to result in an SOA dependent (masking) effect. On the other hand, the percentage values change based on the SOA between the annulus mask and target.

Compared to the set-size 2 condition, in set-size 6 both the baseline cue and mask curves are at a lower level in terms of percentage values. While the set-size 2 values are generally around 80-90% level, the averaged values for set-size 6 are in between 60-80% range. This is already expected since it becomes harder to focus on the spatial domain and perceive the target item rather than distractors when the set-size is increased. Therefore, there is a general decrease in the percentage correct values of set-size 6 as compared to set-size 2, indicating that the modulation of the attentional load in the visual field was valid.

Two-way repeated measures ANOVA was applied to the percentage correct baseline data. ANOVA results show that there is a significant effect of set-size on data ($F(1,7) = 20.08$, $p = .003$, $\eta_p^2 = 0.741$). These results show that our attentional manipulation is effective since the only manipulation in these conditions was the set-size. Moreover, they demonstrate that it was harder for the participants to determine the contour properties of the target stimulus in set-size

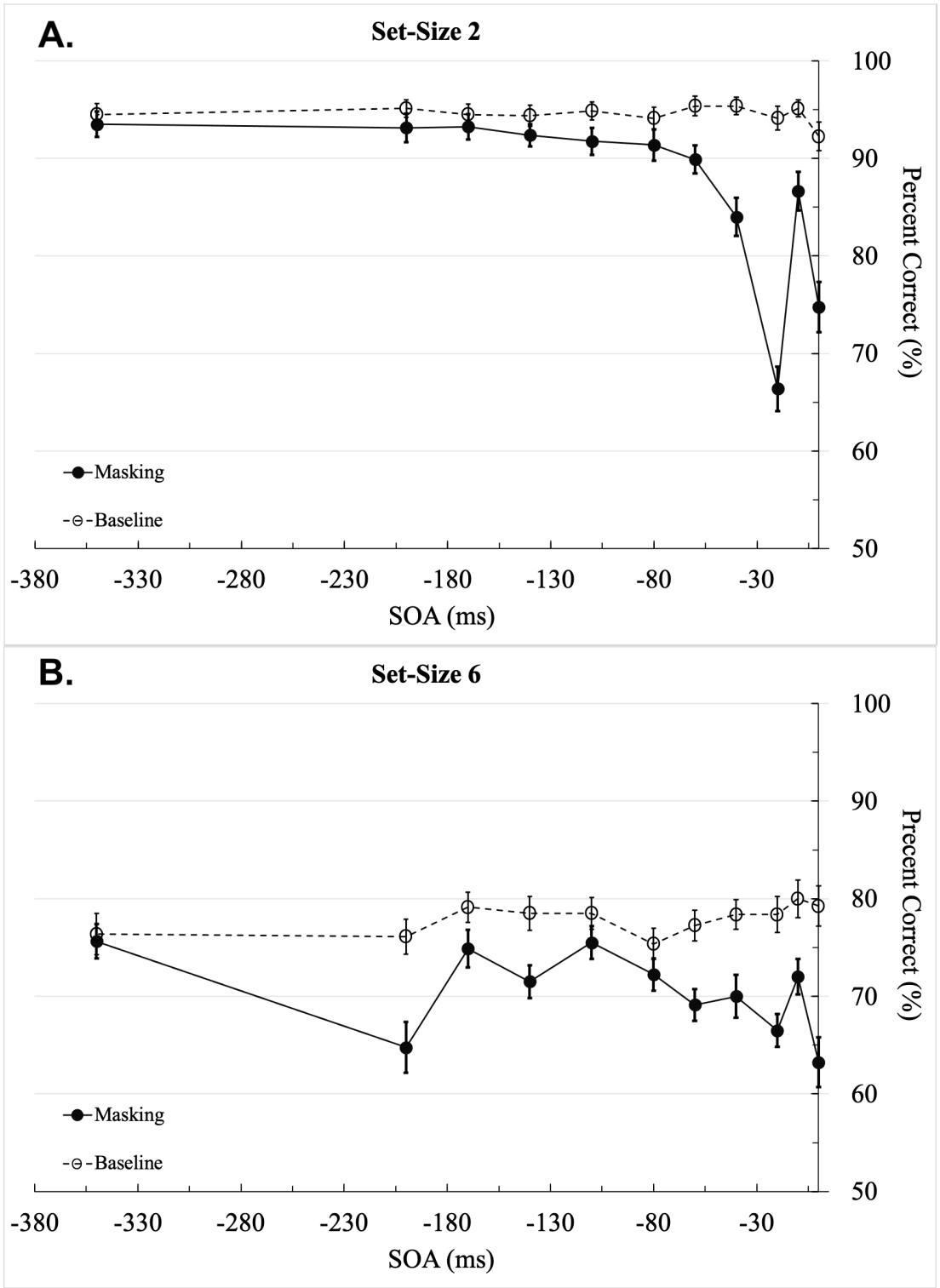

Figure 2.4: **A.** Mean percentage correct values as a function of SOA for set-size 2 masking and corresponding baseline/cue conditions (N=8). **B.** Mean percentage correct values as a function of SOA for set-size 6 masking and corresponding baseline/cue conditions (N=8). Error bars correspond to +/- *SEM*

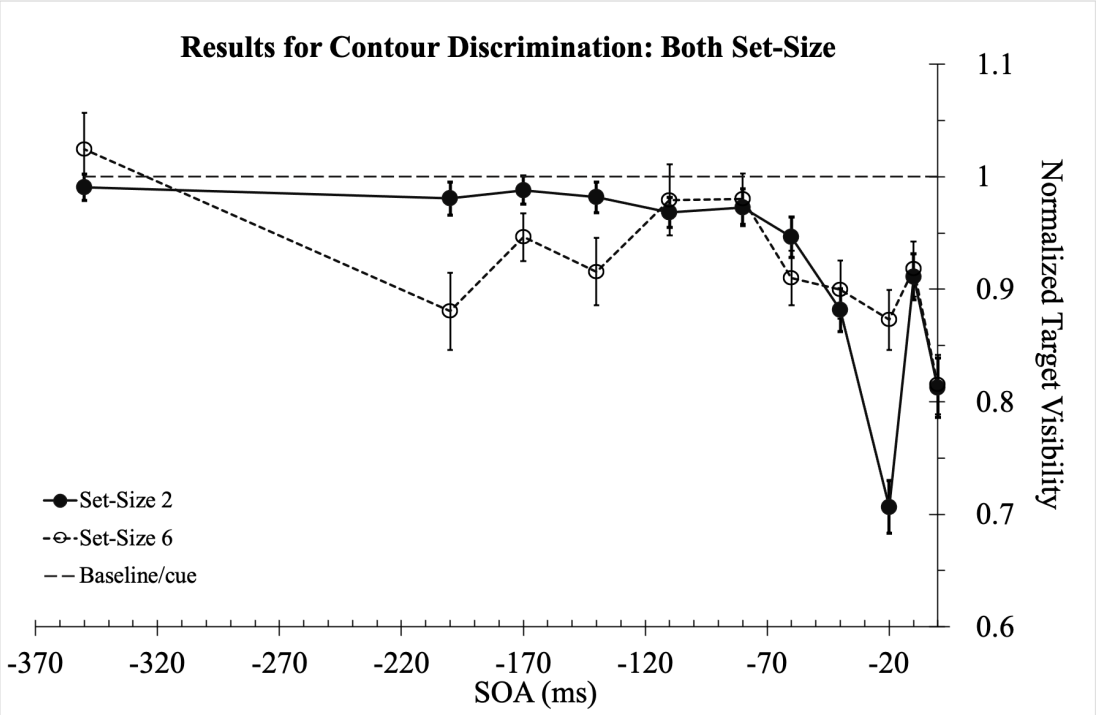

Figure 2.5: Mean normalized target visibility (N=8). The dotted-line represent baseline condition level which is 1 since all conditions were normalized by their corresponding baseline conditions. The continuous line with filled circles represents set-size 2 masking data while the dotted-line with hollow circles represents set-size 6 masking data. Error bars correspond to +/- *SEM*

6 condition due to the increased attentional-load.

To elucidate masking-specific modulations, the percentage values were normalized for each set-size separately (see Figure 2.5). For set-size 2, a large brief inhibition is observed, but there is a quite small prolonged inhibition (also see Figure 2.4.A). On the other hand, a relatively smaller brief inhibition and a larger prolonged inhibition are observed in set-size 6 condition (also see Figure 2.4.B). We performed a two-way repeated-measures ANOVA on the normalized values. The ANOVA test results show that there is a significant main effect of SOA (F (10,70) = 10.85, p =.00, η_p^2 = 0.608) and a significant two-way interaction between set-size condition and SOA (F (10,70) = 2.72, p = 0.007, η_p^2 = 0.280).

Even though, ANOVA analysis on the normalized masking data shows that there is a significant interaction between SOA and set-size, this analysis cannot

give us detailed information about the characteristics of the interaction, (i.e., at which SOA there is a significant dissociation between set-size conditions.) To further understand the source of two-way interaction, we performed comparisons across set-size in the SOA range of brief and prolonged inhibitions. Accordingly, we combined the normalized values in the SOA range of brief inhibition (i.e., 10, 20, 40 ms) and prolonged inhibition (i.e.,140, 170, 200, 350 ms). These criteria and grouping of data were implemented based on both the visualization of the data and the literature [1, 2, 8]. The paired t-tests results indicate that the combined averaged values are significantly different from each other for set-size 2 and set-size 6 conditions. Specifically, for the SOA range of brief inhibition, the set-size 2 condition has a bigger masking effect (M = 0.83, SD = 0.09) than that of set-size 6 [M = 0.90, SD = 0.05, t (7) = 3.02, p = .019, Cohen's d = 1.068]. This particularly suggests that increasing the attentional load in the visual field causes a decrease in the strength of brief inhibition in paracontrast masking. Therefore, one can deduce that spatial attention modulates the processes underlying brief inhibition. According to the dual-channel (RECOD) model, the brief inhibition is caused by the intrachannel inhibition on the sustained channel activation which refers to center-surround antagonistic relationship (i.e., feedforward fast lateral inhibition) within the P-pathway. This explanation is supported by several psychophysical and neurological studies showing that optimal inhibition created by the surround activity on the center activity becomes dominant when the surround is activated 10 to 30 ms before the center activation [67, 68]. Because of this dynamical aspect of a classical receptive field, the surround activation is 10 to 30 ms slower than the center. Therefore, it is expected that the brief inhibition, which occurs when the mask precedes the target around 10 to 30 ms, is due to this center-surround antagonistic (intrachannel) relationship within the P-pathway. Given this interpretation based on the RECOD model, our results suggest that attention has a modulatory effect on the center-surround antagonistic activity within the P-pathway. More specifically, as attentional load decreases and the allocated attentional resource for the target stimulus increases, the strength of the brief inhibition and the inhibitory modulation of surround activity on the center activity within the P-pathway increases.

On the other hand, for prolonged inhibition, the set-size 2 leads to a smaller masking effect (M = 0.9852, SD = 0.03) than set-size 6 [M = 0.94, SD = 0.06,t (7) = -2.44, p <.05, Cohen's d = 0.863]. Notably, the smaller masking effect is represented by better performance values (i.e., closer to the maximum which is 1, since it is normalized based on baseline cue condition) while the larger masking effect is represented by weaker performance. As set-size increases, attentional load increases and the allocated attention for the target decreases; visibility for the target decreases and the masking effect becomes stronger. Hence, attending to a stimulus less makes it more immune to paracontrast masking in short SOA's while more vulnerable against masking in prolong SOA's.

The local minimum of prolonged inhibition is at the -200 ms and it continues up to -350 ms as in a previous study by Breitmeyer and his colleagues [1]. Within the context of dual-channel theory, the prolonged inhibition of the paracontrast is mainly caused by the long-lasting intrachannel inhibitory activation within the P-pathway at the cortical level. This is specifically simulated in the RECOD model through recurrent feedback connections. Therefore, our data suggests that spatial attention modulates this recurrent processing at the cortical level. There are several neurophysiological studies showing long-lasting cortical inhibition is occurring in the visual cortex of different species [69, 70, 71]. In these studies, they found that there are cells showing inhibition around 200 ms ISI. These findings support our results and also the predictions of the RECOD model on the long-lasting cortical inhibition. Therefore, it may be inferred from our data that increased attentional load increases the slow intrachannel inhibition of the P-pathway and is mainly carried out at the cortical level.

Chapter 3

Attentional Effect on Facilitation of Paracontrast Masking (Experiment 2)

This chapter is dedicated to the second experiment of this thesis. As mentioned before, the main question (whether and how spatial attention modulates paracontrast masking) is divided into two sections and studied by separate tasks due to the fact that inhibition and facilitation components of the paracontrast masking have been mainly observed through different experimental tasks [1]. Therefore, in the second experiment, the aim is to further study the facilitation component of paracontrast and to examine the potential modulatory effects of attention. Using a similar logic with the first experiment, it is hypothesized that if set-size manipulation is added on top of the perceived brightness judgment task, it is possible to study both paradigms together to study their relationship.

In the case of the interaction, attentional manipulation will change the characteristics of the facilitatory process, e.g., by changing the location or the magnitude of the extrema (maximum in this experiment, minima in the first experiment).

If attention and facilitation are independently running processes, then we

would not expect to see any changes in the characteristic features of the paracontrast masking function under various attentional-load conditions. In this case, the function of perceived brightness depending on the SOA conditions might be shifted up or down a little bit, but since baseline correction is used, this will not affect the normalized masking function at the end. Accordingly, it is expected to observe no differences between conditions.

Based on the previous literature on the functional correlation between attention and subcortical structures [72], we expect to observe an interaction between attention and facilitation component.

3.1 Method

In this experiment, perceived brightness judgment was used given that a former study showed that the facilitation component becomes dominant for this task rather than the contour discrimination task [1]. Perceived brightness was represented in luminance values (cd/m^2) and calculated by taking average luminance values of the last 6 reversals out of 9 in a 1-up 1-down staircase procedure. Step sizes were 4 units for the first three reversals, and 10 units for the rest while a unit of step corresponded to 0.45 cd/m^2 change in the brightness/luminance [total reversal number, step size, and the number of averaged reversals are defined based on the study by Kafalıgönül et al. [2], but still tested using several different parameters during the pilot studies].

It is aimed to explore the effects of attention on the facilitation component of the paracontrast masking. However, personal differences, mentioned as criterion content in the introduction, may cause different masking functions. Additionally, some subjects may not perform the task well enough which causes too much noise in the data. Thus, we needed participants who produce a masking function with a facilitation component, when no attentional manipulation is added to the design. Hence, an additional condition to the first experiment, a set-size of 1 was implemented to control the procedure and effectiveness of the task for each

participant.

To make sure that our staircase and perceived brightness judgment task are able to replicate the facilitation findings in the literature [1, 2], a pre-experimental study was conducted. Additionally, to identify effective luminance values and have an efficient design, a pilot study was also performed. Both pre-experimental, pilot studies, and the main experiment will be described below.

3.1.1 Participants and Apparatus

Seven subjects (age range: 19-33 years) participated in the main experiment while three subjects participated in the behavioral pilot studies; two of which also took part in the main experiment. All participants had normal or corrected-to-normal vision. Informed consent was signed, and the prescreening form was filled by each participant before starting the experiment. The apparatus and testing room were the same as the first experiment.

3.1.2 Stimuli and Experimental Design

For the target, distractor, and comparison stimuli, identical shaped (filled, round with a diameter of 1°, and gray) stimuli are used. But they were slightly different in terms of their brightness. Luminance values for target stimulus were 40 cd/m^2 and 30 cd/m^2, respectively for the pre-experimental study and main experiment; and changed across trials for comparison stimulus. Annulus/ring-shaped stimuli, whose thickness is 0.2° and surrounding circle stimuli, were used as the mask. In the masking condition of the main experiment, masks encircle the target and distractors, but not the comparison. A small black square with 0.2° side length was used as the cue (see Figure 3.1C). In the baseline condition of the main experiment, cues were presented at the locations of the target and distractors. Rather than using target-only conditions, using cues as the baseline is more proper for paracontrast masking to control a possible cueing effect of the preceding mask.

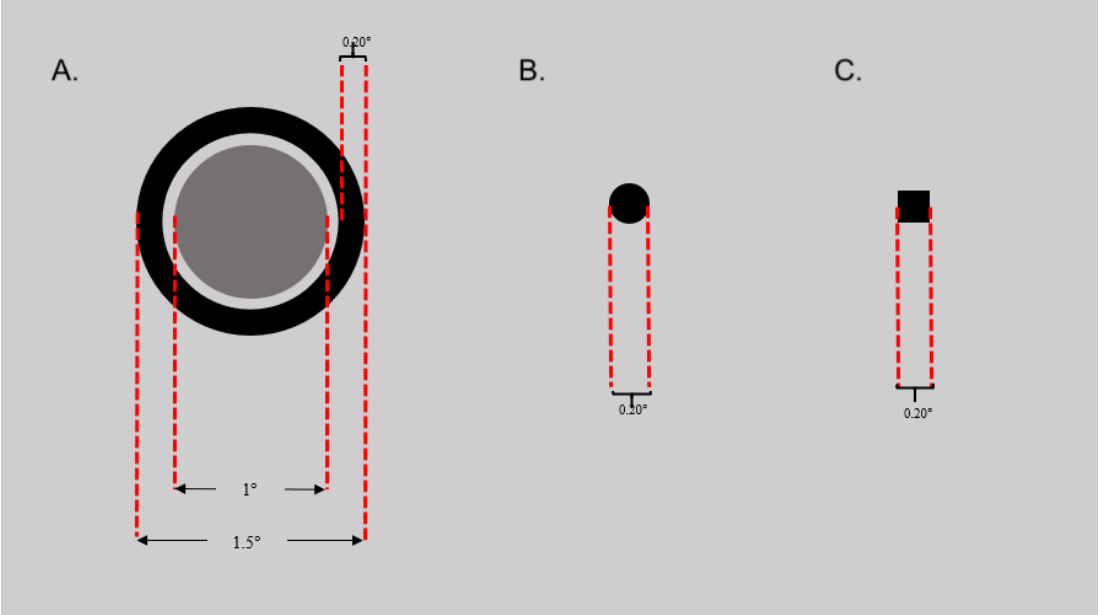

Figure 3.1: **A.**The target and mask stimuli. The target (or distractor) was placed inside the mask ring. **B.**The fixation point. **C.**The black cue.

The black cue and the mask had the same luminance value of 1.3 cd/m^2 for the pre-experimental study and 15 cd/m^2 for the main experiment. All stimuli are described in Figure 3.1 The background luminance value was 80 cd/m^2 and 65 cd/m^2 for the pre-experimental study and main experiment, respectively. Additionally, during the pilot study (see 3.1.2.0.2 Pilot Study) these values were optimized, and the best parameters were chosen to reflect the characteristics of paracontrast masking. Specifically, pre-experimental study and pilot study differ in terms of what features of the experimental design are optimized.

3.1.2.0.1 Pre-Experimental Study To ensure that the 1-up 1-down staircase procedure was working, and that the facilitation component was reflected [1, 2], we initially conducted a pre-experimental study. Its basic design is described in Figures 3.2 and 3.3. In this study, we had 2 same-sized, filled, round shape stimuli at both right and left sides of the fixation point (Figure 3.2). The stimuli were placed at equidistant locations and presented simultaneously for 20 ms. There was a masking condition including a surrounding ring stimulus for the target stimuli and a baseline (target-only) condition. Mask stimulus was also

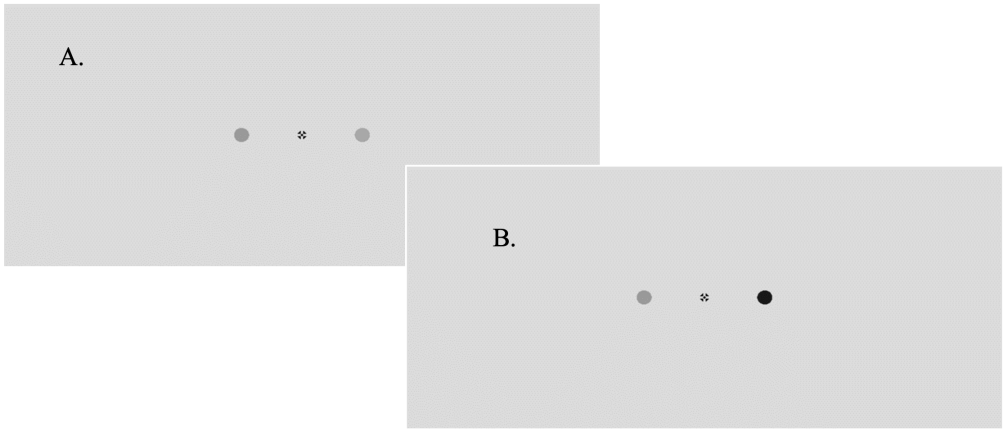

Figure 3.2: An exemplar trial for the baseline(target-only) condition of the pre-experimental study.**A.** In this example, the comparison stimulus is brighter (right one) **B.** The target stimulus is brighter (left one). As one can easily notice, the target stimulus (left side) always has the same brightness level while comparison stimulus is changing according to the response of the previous trial.

presented for 20 ms. There were several SOA conditions (40, 60, 80, 110, 140, and 170 ms) referring to the relative timing between mask and target, for masking (i.e., mask-target) trials. The baseline trials included only target and comparison stimuli simultaneously presented at the two sides of the fixation point (Figure 3.2).

The mask-target trials included a ring stimulus presented for 20 ms and the target and comparison stimuli appeared after a specified time of SOA (Figure 3.3). The participants were requested to indicate which stimulus was brighter via keyboard press (i.e., the one on the right or left side, the target or comparison). The luminance value of the target stimulus did not change from trial to trial while the brightness of the comparison stimulus was adjusted after each trial by increasing or decreasing according to the observer's response. A reversal was defined as giving a response that is different from the previous trial. The fixation was the same as the one in the first experiment (see 2 Attentional Effect on Brief and Prolonged Inhibition of Paracontrast Masking). Several luminance values were tried to find the effective parameters (i.e., increments and decrements), and the values mentioned in the previous section (see 3.1.1 Participants and

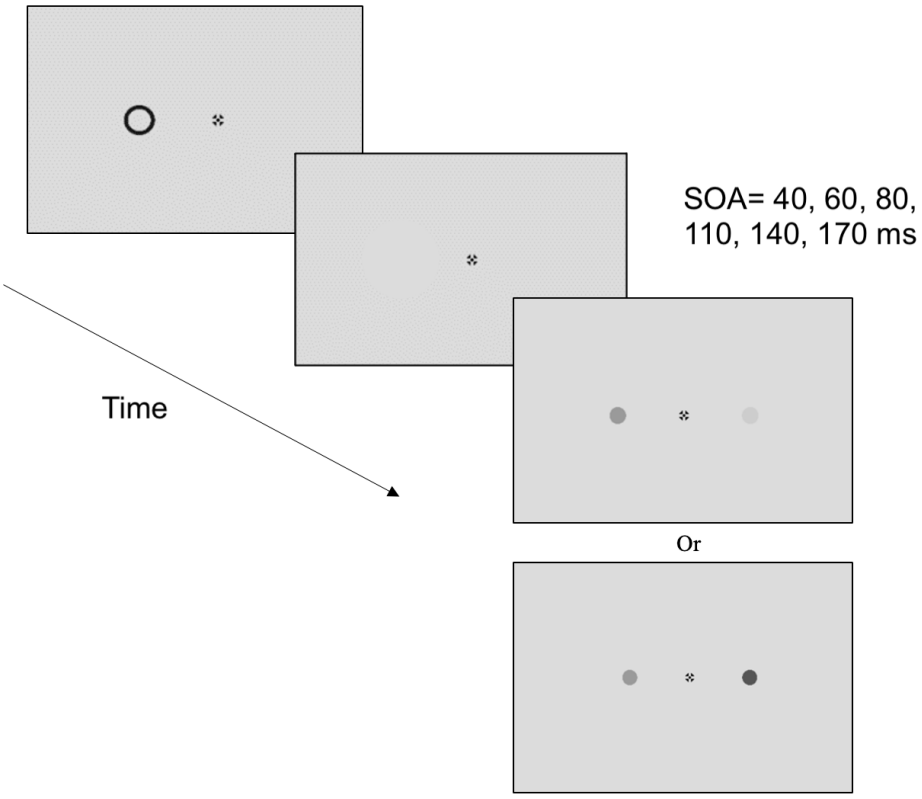

Figure 3.3: Exemplar trial for the mask condition of pre-experimental study. A ring surrounding the target was presented and then a blank screen was presented for a specified SOA duration. Then, target (left) and comparison (right) were presented simultaneously. Target stimulus always had the same brightness while comparison stimulus might be brighter (upper screen) or darker (below screen) than the target. The task was to decide which one was brighter. After a response (keyboard press), the brightness of comparison stimulus was increased or decreased accordingly.

Apparatus) are accepted.

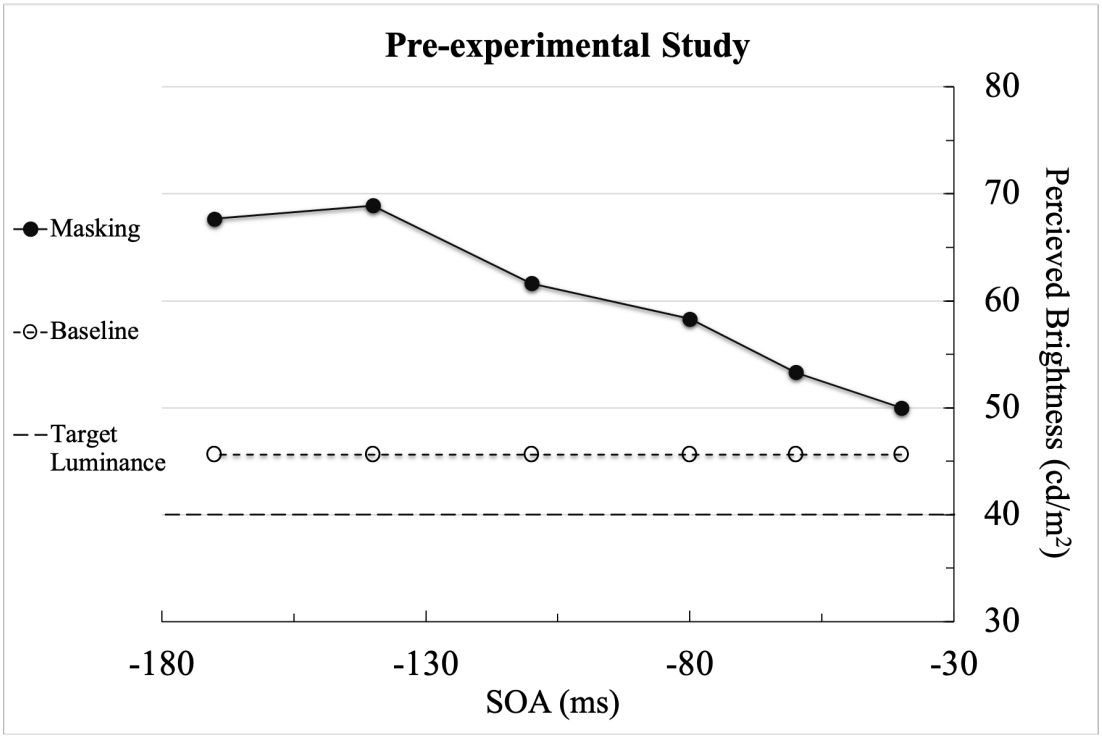

Figure 3.4: The perceived brightness values in cd/m^2 for mask and baseline (target-only) conditions of the pre-experimental study.

In Figure 3.4, the perceived brightness values in cd/m^2 for mask and baseline (target-only) conditions (n=1) can be seen. Even though there were representative SOA conditions and a limited number of participants and repetitions, the facilitation component is evident. It is indicated in the literature that this enhancement is seen between -140 and -20 ms which is consistent with these preliminary findings ([8] p. 43).

3.1.2.0.2 Pilot Study After the staircase procedure and its parameters were optimized, the experimental design was further developed by adding attentional manipulation using set-size conditions as in the previous experiment (see 2 Attentional Effect on Brief and Prolonged Inhibition of Paracontrast Masking). This step included several pilots with different experimental designs and parameters to reach optimal ones (location of the comparison stimulus, temporal properties

of the screens and stimuli shown in Figures 3.5, 3.6, and 3.7, etc.). The accepted design and parameters for the main experiment are described below.

3.1.2.0.3 Main Experiment We used 2x2x7 design representing 2 attentional conditions (set-size 2 and set-size 6), 2 experimental conditions (mask and baseline cue) and 7 SOA conditions (0, 10, 20, 40, 60, 90 and 120 ms). The normalization of the masking data to the corresponding baseline/cue data eliminated possible confounding factors and revealed specific masking strength for each set-size and SOA condition. In the practice session, we used a set-size 1 condition to train each participant to the main task and paradigm. SOA values were selected based on the findings that the facilitation component occurs, and the validity of this range was also confirmed with the experimental pre-study ([8] p. 43, and [1, 2, 13]. The timeline of a trial is displayed in Figures 3.5, 3.6, and 3.7 for set-size 1, set-size 6, and set-size 2 conditions, respectively.

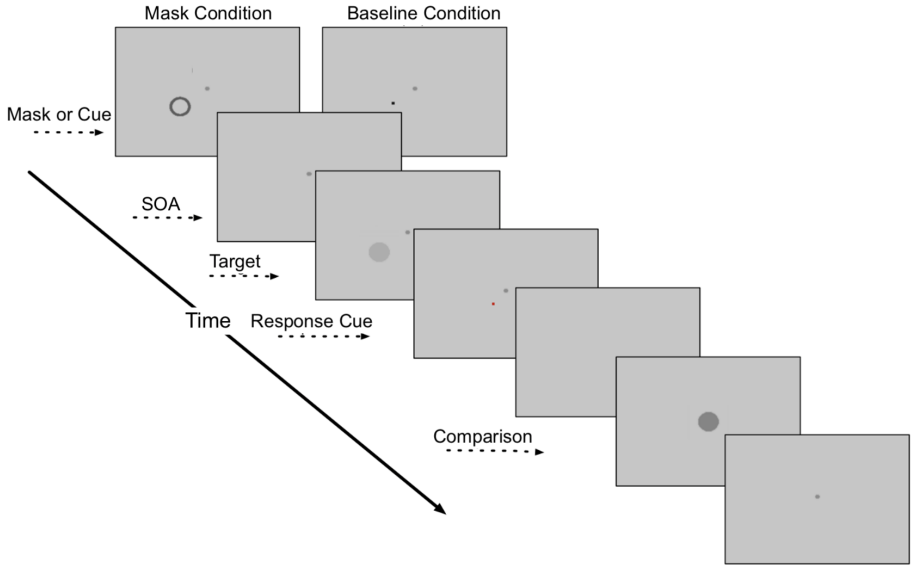

Figure 3.5: The timeline of an exemplar trial for set-size 1 condition.

Similar to the first experiment (2), the mask and target (and other distractors) stimuli were placed on an imaginary circle with a 4° diameter centered to the fixation point while baseline cues were placed on an imaginary circle with 2°

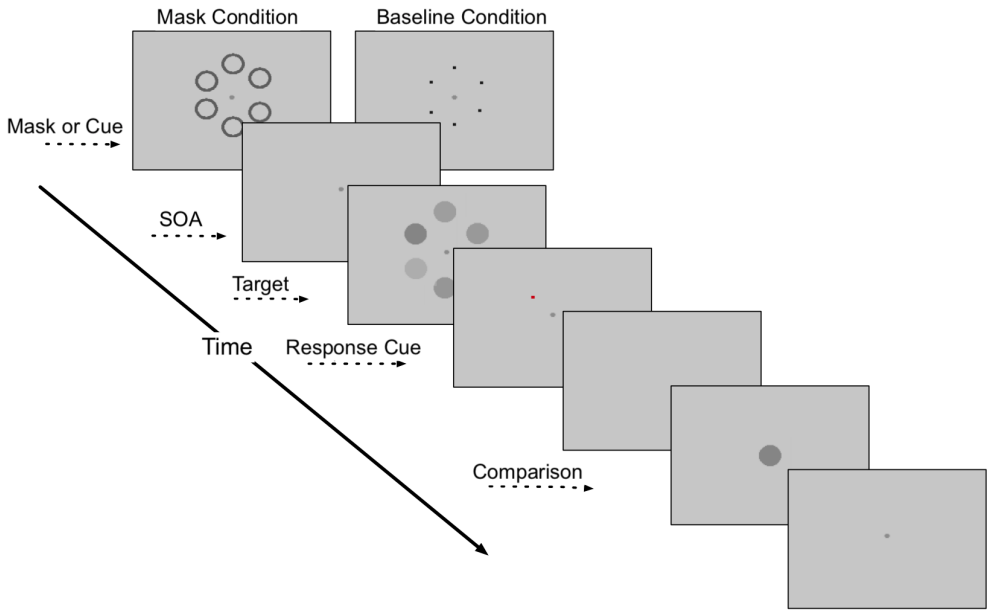

Figure 3.6: The timeline of an exemplar trial for set-size 6 condition.

diameter centered to the fixation point. The final response cue was placed on an imaginary circle with 1.2° diameter centered to the fixation point. All stimuli stayed on the screen for 20 ms. We separated the set-size conditions (set-size 2 and 6) and mask-baseline (mask and baseline-cue) conditions into 4 different blocks. Within a block, all SOAs for the selected set-size and mask type were randomized. The perceived brightness of the target under each SOA condition was estimated through adaptive staircase procedure and thus the number of trials for each condition was not fixed. Each trial started with a blank screen for a random time between 500 and 1000 ms. Then, based on the condition, either a cue or mask screen was presented for 20 ms. A cue or mask screen included 1, 2, or 6 cues or masks, depending on set-size condition. After an SOA, the target screen was presented. A target screen included a target and distractors. The distractors had the same shape as the target. Although the luminance value (brightness) of the target (30 cd/m^2) did not change, each of the distractor stimuli had a brightness value that was slightly and randomly different from the target's brightness (30±5 cd/m^2). The location of the target stimulus changed for every trial so that all stimuli in the target screen had an equal possibility to be the target stimulus. 100 ms after the target screen, a response cue (i.e., a small red

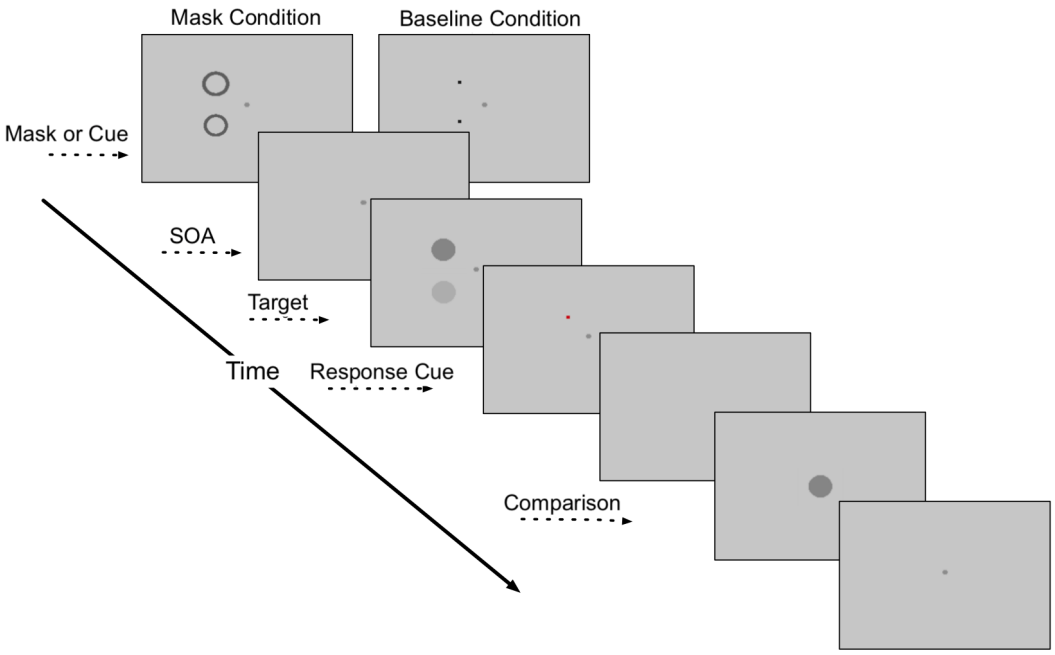

Figure 3.7: The timeline of an exemplar trial for set-size 2 condition.

square) having the same shape as the baseline cues were presented for 150 ms to indicate the location of the target stimulus. At the end of the trial, the fixation point disappears for 300 ms to eliminate a possible masking/interaction with the following stimulus (comparison stimulus). The comparison was presented at the center for 20 ms. As mentioned above, before and after the presentation of the comparison stimulus, there were 300 ms blank screens (without a fixation point). The comparison stimulus had the same shape as the target and distractors. For the first trial, the brightness of the comparison was assigned randomly from a range of values starting from a value of 2.5 cd/m^2 to 38 cd/m^2. Therefore, the comparison stimulus was always darker than the background, having the same polarity as the target. Even in the staircase procedure, the contrast polarity of comparison was preserved. After the comparison stimulus and before the presentation of the fixation point (response screen), another 300 ms blank screen was presented to eliminate any possible interaction of fixation and comparison stimulus. To eliminate any possible interaction and masking, we also changed our fixation point from bulls-eye to a single small filled-circle with 0.2° diameter. The response screen included only a fixation point and was presented until the

		Experimental Conditions					
		set-size 1		set-size 2		set-size 6	
		masking	baseline(cue)	masking	baseline(cue)	masking	baseline(cue)
Sessions/Days	1st and 2nd sessions	2 repetition	2 repetition				
	rest of the 4 sessions			1 repetition	1 repetition	1 repetition	1 repetition

Figure 3.8: The distribution of the experimental conditions on the blocks and sessions. Each baseline or masking block had all of the SOA conditions.

participant responded. The participants were requested to indicate which stimuli appeared brighter. The brightness of the comparison stimulus was changed for the next trial based on the participant's response. When a participant responded that the comparison was brighter, the luminance of the comparison was increased by 4.8 cd/m^2 and 1.92 cd/m^2 for the first three reversals and all of the rest, respectively. Conversely, the brightness of comparison was decreased using the same step size. If the participant gave a response that was different from the previous, it counted as a reversal. After 9 reversals, the average brightness value of the comparison stimulus during the last 6 reversal was calculated as the perceived brightness value of the target stimulus for a specific condition.

5 or 6 sessions were run throughout the experiment (see Figure 3.8). Each session was run in a single day and consisted of 4 blocks (2 set-sizes x 2 mask types) of trials. As mentioned in the previous sections, the participants also attended 1 or 2 training sessions consisting of baseline and masking blocks for set-size 1. In general, 2 sessions (4 repetitions) of the set-size 1 conditions were applied to the participants both to improve their task performance and reduce the noise level, and to be consistent with the 4 repetitions of other set-size conditions. After the training sessions, if a participant met the requirements, then he/she attended the main experimental sessions.

3.2 Data Analysis

At the end of each session, the perceived brightness values in cd/m^2 for all the SOA conditions were calculated. For each participant, SOA and set-size, we normalized the values of annulus mask conditions with those of corresponding baseline (cue) conditions. Based on the normalized values of the training session (i.e., set-size 1), the participants were expected to meet the following criteria:

1. Having a facilitation component in the SOA range of around 10-100 ms.
2. Generating a masking function without having extensive oscillations/ripples dominating the overall morphology and main characteristics of paracontrast. In a basic design of set-size 1, we wanted to make sure a robust facilitation component in paracontrast masking so that we could differentiate the effects of spatial attention in the main experiment.

Once a participant met the criteria of the training session, the main experimental sessions were conducted. At the end of the experiment, there were 4 data sets for each condition (2 set-size x 2 mask type) each consist of seven data points corresponding SOA values. For each set-size condition of a session, the masking data of all SOAs were normalized with the corresponding baseline cue. After the normalization, 4 normalized masking data sets were corresponding to 4 repetitions (sessions) for each set-size condition. These normalized masking data were averaged across sessions of a participant. A two-way repeated-measure ANOVA (with set-size and SOA as factors) was carried out with the averaged normalized values.

3.3 Results and Discussion

Figure 3.9 shows the mean perceived brightness and normalized values for set-size 1 (i.e., the training session). Subject variability (e.g., the variation in the peak

facilitation) led to an overall for almost all SOAs in the group-averaged data. Figure 3.10 also shows the mean perceived brightness values for set-size 2 and set-size 6.

Figure 3.11 shows the results of normalized brightness values for set-size 2 (continuous line with filled circles) and set-size 6 (dotted-line with hollow circles) conditions of the main experiment. The plots indicate that that set-size 2 condition does not lead to a facilitation component dependent on SOA while set-size 6 condition leads to a masking function highly similar to those reported by previous studies [2, 1]. A local maximum of around -60 ms of SOA is in line with previous reports. Additionally, a brief inhibition in the function of set-size 6 is observed. We performed a two-way repeated-measures ANOVA on this dataset. The ANOVA test did not reveal any main effects (SOA: $F(6,36) = 1.28$, $p = .289$, $\eta_p^2 = 0.176$, set-size: $F(1,6) = 0.05$, $p = .838$, $\eta_p^2 = 0.008$) or a two-way interaction ($F(6,36) = 1.50$, $p = .207$, $\eta_p^2 = 0.2$). The lack of non-significance SOA effect might be mainly driven by the flat curve of the set-size 2. Accordingly, we also performed one-way ANOVA on the data from set-size 6. Similarly, although p-value is quite smaller than former test, we could not find any significant SOA effect for set-size 6 data ($F(6,36) = 1.824$, $p = .122$, $\eta_p^2 = 0.233$).

Based on the outcome of these statistical tests, one can conclude that our experimental design is failed to reveal paracontrast facilitation components since SOA is a critical experimental factor for paracontrast and facilitation. Hence, comparisons across set-size conditions may not be meaningful. In our experimental question, the key factor is paracontrast-based facilitation, which typically peaks around negative 90 to 60 ms SOA. Therefore, it is critical to make sure a robust facilitation component in the main experiment. However, as indicated before, our results failed to produce significant differences between SOA conditions which shows that there might be a problem in creating paracontrast masking function (and its facilitation component) in the first place. Despite our effort to control subject variability and other potential confounding factors, the lack of significant SOA-dependent facilitation might show a deficiency in the design. We speculate that the experimental design might be too complicated in terms of

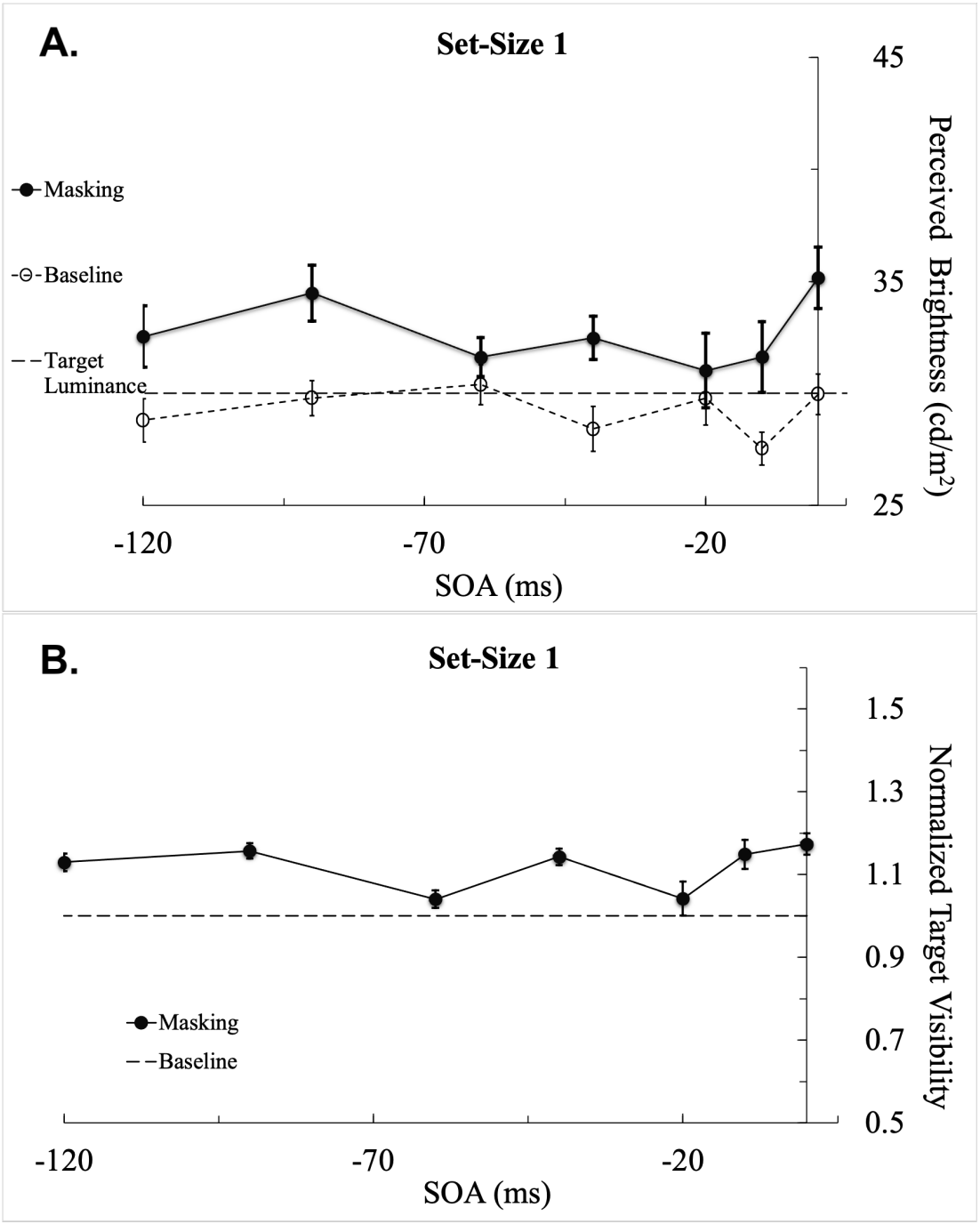

Figure 3.9: The mean perceived brightness values for set-size 1 (training) condition (n=7). **A.** The filled circles represent the data of masking condition while open circles display baseline(cue) condition values . **B.** The perceived brightness values for masking conditions normalized by the corresponding baseline (cue) condition. Error bars correspond to +/- *SEM*

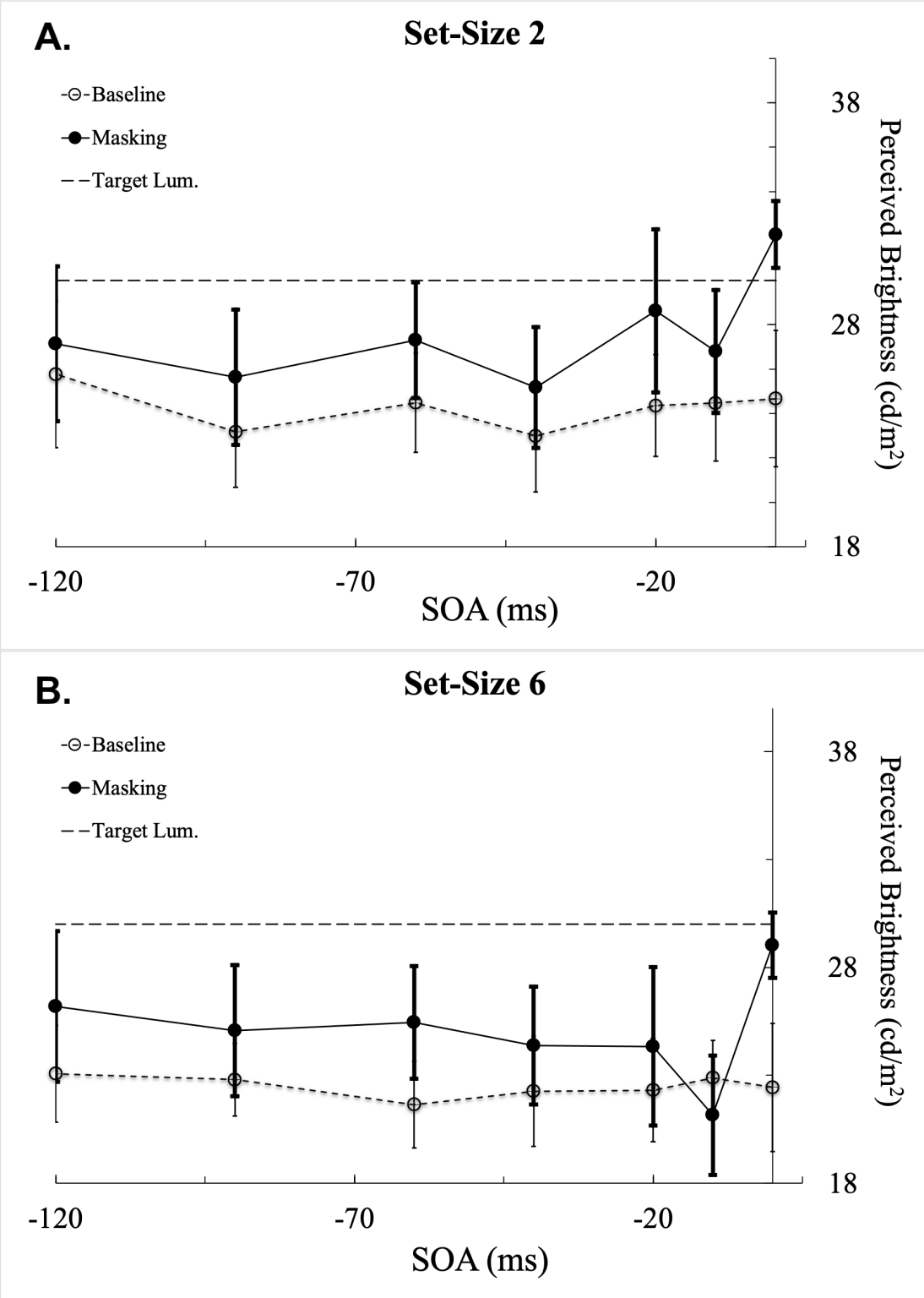

Figure 3.10: The black line represents masking condition while the gray line represents baseline(cue) condition. Data points represent luminance values in cd/m^2 for corresponding SOA (n=7). **A.** Set-size 2 . **B.** Set-size 6. Error bars correspond to +/- *SEM*

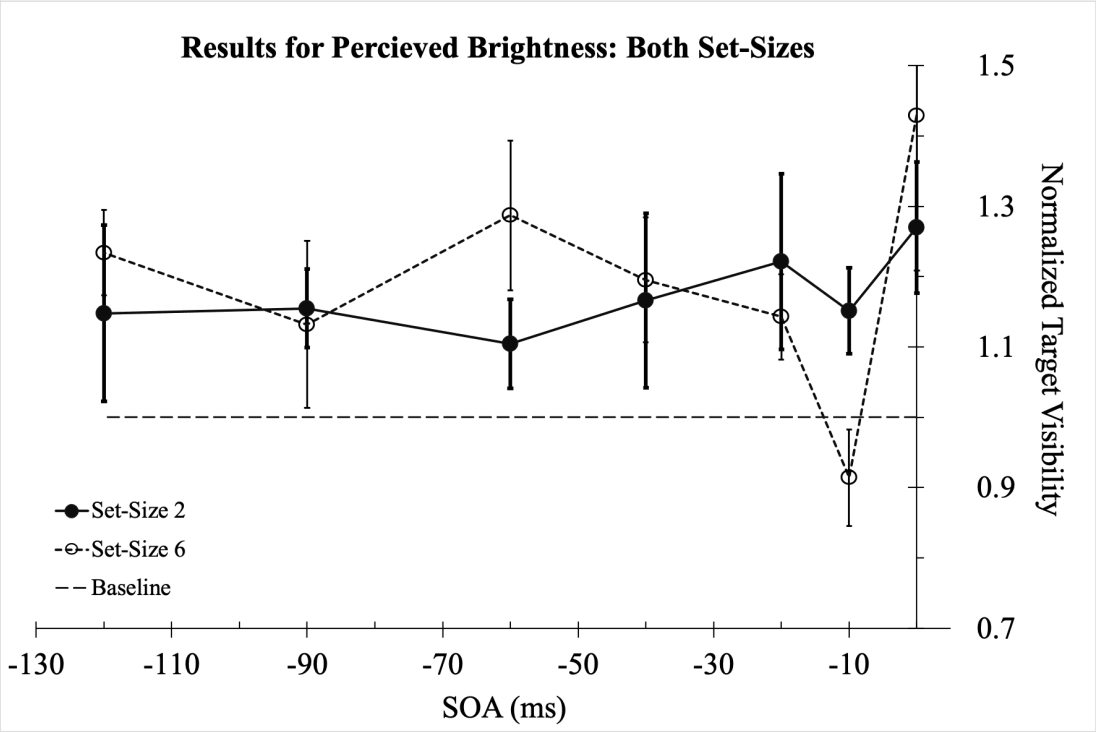

Figure 3.11: The normalized target visibilities for set-size 2 and 6 conditions (n=7). The filled and open circles display the data of set-size 2 and 6 conditions, respectively. The dashed line represents the baseline(cue) level. Error bars correspond to +/- *SEM*

the number of screens such that participants could not follow instructions and perform the perceptual task.

To improve the design, in further behavioral studies, we are planning to simplify the task by decreasing the number of blank screens and putting both the target and comparison on the same screen. A possible confounder of memory may be prevented by applying such changes; since the current design included a 500 ms duration between the compared stimuli (i.e., target vs. comparison). Also, presenting comparison and target stimuli at different locations (i.e., presenting the comparison at the center/foveal and presenting the target as peripheral) may be an additional confounding factor. Since brightness/contrast matching is relatively harder to perform, having a bigger target and comparison stimuli may also be helpful. In an elaborated design, testing the effects of these changes on the facilitation components will be informative.

Chapter 4

General Discussion

4.1 General Discussion

Throughout the day, lots of information enters the visual system. Some of them are useless at that moment while some of them may have survival value. Therefore, the system needs to have a selection process. Attention has been considered as the process of selectively filtering irrelevant information. As mentioned before (in Section 1.2.5 Attention and Memory), this filtering is hypothesized to happen during the information transferring process from iconic memory to VSTM (see Leaky Hourglass Analogy of Öğmen et al.[13]). On the other hand, visual masking is also known for filtering the information transferring from iconic memory to VSTM. Accordingly, an important question to ask is whether two of these filtering/selection processes controlling the flow of information from sensory memory to VSTM interact or not. Additionally, since several theories are suggesting underlying neural mechanisms for both attention and visual masking, a possible interaction or independence between them is also informative in terms of understanding the connections/processes in the visual system. Investigating the effects of attention on paracontrast masking is also important to test the predictions of proposed theoretical models for visual masking. Although there are several studies examining the possible interaction between attention and different types

of visual masking ([9], and mostly for metacontrast masking: [3, 33]), as far as we are aware, there is no investigation on the relationship between attention and paracontrast masking.

Based on the SOA range, three components have been proposed for paracontrast masking: brief inhibition, facilitation, and prolonged inhibition [2, 1, 8, 73]. The inhibition components decrease the visibility of the target stimuli. While brief inhibition occurs at early SOA's, the prolonged inhibition occurs at late SOAs and can be sustained up to -400 ms. The facilitation reflects a component of the paracontrast masking function that represents an increase in the visibility of the target stimuli typically peaking around -60 ms. Previous studies have revealed that parameters and criterion contents significantly change the masking functions which were described in Chapter 1. For instance, , a previous study [1] showed that different perceptual tasks make distinct components of paracontrast masking dominant. In that study [1], it is indicated that contour discrimination tasks cause inhibition components of the paracontrast while brightness judgment (surface-based) tasks result in facilitation component. Thus, using a contour judgment task, we aimed to elicit brief and prolonged inhibitions. Then by adding set-size conditions, the attentional load was modulated. An increase in the set-size is expected to decrease overall performance. Taking together (the paracontrast masking function with brief and prolonged inhibition components and various attentional conditions), it is possible to see whether the modulation of the attention through set-size conditions causes a distinct modulation in the paracontrast masking function (as in Figure 1.11) or not. If attentional manipulation in the visual field differentially modulates the paracontrast masking function, then one may conclude that there is an interaction/dependency between attention and paracontrast masking, in the SOA range of brief and prolong inhibition components. Moreover, using visual masking as a tool to study attentional mechanisms is a good way to study time dynamics of the neural correlates of attention. In this way, we can get informed about the early and late attentional processes and their hypothesized locations in the brain.

First of all, as indicated by Figure 2.4, increasing attentional load causes a decrease in the overall performance for baseline conditions. This is an expected

result due to the previous studies showing that increased set-size leads to an overall performance decrease [74]. Attention has limited capacity. Even though it selects the target information and directs all of its resources to it; for this task, all of the stimuli given in the target screen had an equal probability of being a potential target or one of the distractors. Accordingly, the participants had to distribute attention to all stimuli (two or six of them). This reduced the overall resource that was directed to the target stimulus in the set-size 6 conditions, compared to the set-size 2 conditions.

Results show that attentional load significantly modulates the inhibition components of the paracontrast masking function (Figure 2.5). Thus, one can infer that attentional processes interact with the inhibition components of the paracontrast. More specifically, as showen in the results of the first experiment, the small set-size condition leads to an enhancement of brief inhibition and reduction in the prolonged inhibition. These interactions can be explained by an already existing theoretical model (RECOD) which was initially proposed to explain "non-linear feedback processes" and illustrates the trade-off within the visual system caused by the conflicting feedforward and feedback signals [75]. The model was elaborated on later to extend its scope to further explain the dynamics of the visual system [1]. It is also supported by several psychophysical and neurobiological studies/findings [8]. The RECOD model suggests that brief inhibition is produced by the early intrachannel inhibitory (e.g., lateral) interactions within the P-pathway. There is an interaction between the excitatory center activation of the target and the inhibitory surround activation of the mask. This is evident by the observation that every stimulus, both the target and mask stimulate the sustained and transient channels, and the RECOD model demonstrate between channels and within channel inhibitory interactions. This interaction leads to a decrease in the target visibility at an optimal SOA between 10-30 ms. This suggestion has been supported by several neurophysiological studies showing that center activation is approximately 10-30 ms faster than inhibitory surround activation [68, 67]. Furthermore, our results indicate that attentional processes take place in this low-level ON center- OFF surround receptive field-based inhibition/interaction within the sustained channel (P-pathway). Attention has a

modulatory effect on the classical center-surround RF interaction at both the pre-cortical and cortical stages. When there is more attentional resource, brief inhibition increases. It means that either the surround inhibition is increasing, or the center enhancement is decreasing.

On the other hand, the brief inhibition component of the paracontrast masking founded in the literature might be dependent on the existence of the attentional resources. When attentional resources are reduced by increasing the attentional load, the antagonistic relationship of the center-surround RF does not reduce the target visibility significantly. This relationship is modulated by attention so that it either increases the center enhancement, or decreases the surround suppression. Attentional modulation on brief inhibition shows that attention modulates visual input/processing at the early stages of visual processing. Attentional modulations are known to be effective as early as dLGN [76]. This conclusion is also supported by a previous study illustrating that attention increases the synaptic efficiency of dLGN neurons on V1 projections [77]. Also, since "attention directly enhances the sensory information processing by enhancing the ratio of signal-to-noise in neural circuit communication" [77], both the input coming from mask and target stimuli are enhanced, and their interaction may cause a bigger effect, as our findings suggest.

In the case of the prolonged inhibition at late SOAs, it is explained by the RECOD model as a result of the long-lasting cortical interactions (i.e., mainly recurrent) through P-pathway [1, 8]. Our results show that increased attentional allocation to target stimulus reduces higher-level cortical inhibition within the P-pathway which is hypothesized as the main underlying mechanism of the prolonged inhibition. When attentional load increases, prolonged inhibition also increases. Therefore, one can infer that there is an interaction/dependency between attention and prolonged inhibition of paracontrast. Probably feedback connections play a role in this high-level interaction.

Attention is known as modulating the cortical activity and/or sensory perception via top-down/feedback signals [76, 78, 18]. The prefrontal cortex (PFC) is claimed to be responsible for top-down attentional modulations. But there

is an ongoing debate on whether it inhibits irrelevant information or enhances the activity for relevant information [79]. Whereas the earlier studies propose that attention inhibits the irrelevant information via PFC; Egner, and Hirsch [80] found in an fMRI study that increased attention amplifies the relevant input but does not inhibit the irrelevant ones. They also showed that this cognitive control is mediated by the dorso-lateral Prefrontal Cortex (dlPFC). Therefore, these results support our findings showing that increased attention decreases the visual masking which is hypothesized to be caused by the cortical inhibition due to the cortical interactions/inhibitions. If the attention is using an inhibition mechanism rather than an enhancement mechanism to modulate the information in the system, then we would expect to see a higher masking effect and stronger prolonged inhibition for the high-attentional-load condition. Because, the inhibitions in the system would be added to each other and create a bigger inhibition. However, we see smaller inhibition on the visibility of the target when set-size is smaller (this condition reflects high-attention).

As briefly mentioned in Chapter 1. Introduction, besides the hierarchical structure and feedforward signaling, recurrent and feedback projections from higher-level areas are also crucial in the visual system. The role of feedback signals is emphasized by recent models and studies ([81, 82]; see [78] for review). Earlier attention studies claimed that top-down and bottom-up attention were mainly mediated by feedback and feedforward signals, respectively. Moreover, it was claimed that the top-down modulation (feedback) of attention takes a long time since it is a higher-level process and needs more time to reach higher-level areas, to be processed, and to come back. So, former theories assume that top-down attention cannot modulate bottom-up attention (feedforward). Similarly, bottom-up attention is hypothesized to stand mainly on feedforward processes since it is assumed that feedback processes take time. However, Khorsand et al. [78] challenged this perspective by presenting results from a recent computational study [81]. The simulation results indicate that bottom-up attention does not occur only due to the feedforward signals; rather, bottom-up attention also depends on feedback information from higher-level areas. Based on these findings, Khorsand et al.[78] also point out that feedforward processing occurs

by slow-dynamic NMDA-receptors while feedback processing occurs on a successive layer by fast-dynamic AMPA-receptors. Hence, feedback signals can have a chance (temporally) to modulate the feedforward signal.

Additionally, a study found that the existence of distractors (rather than only the target) causes signal enhancement through feedback mechanisms corresponding to the top-down modulation on bottom-up processes in early areas [76]. Another study emphasizing the feedback signaling in the visual system found that attentional modulation reaches FEF (frontal eye field) firstly (starting at 80 ms), and then reaches V4 (starting at 130 ms after cue onset) [83]. These findings not only corroborate the feedback projection in the visual system but also gives a timeline of the attentional activation and modulation. For example, considering the route of feedback modulation from higher-level areas (i.e., FEF) to the lower-level areas (i.e., V4), one may predict that this activation may reach V1 after V4, around 200 ms.

In the case of our study, based on Moore and Armstrong's findings [76], feedback enhancement increases more in set-size 6 conditions, due to the increased set-size. Based on the study of Gregoriou et al [83], this increased attentional modulation might reach the V1 level after 200 ms. Therefore, it might be the case that in the set-size 6 condition, mask stimuli creates a signal which is enhanced by the higher-level areas more than in the set-size 2. Then, this increased signal may come back to V1 around 200 ms when the target stimulus is presented (SOA=200 ms). Thus, at low-level visual areas (i.e., V1), the attentionally enhanced feedback signal of the mask can inhibit the target's visibility at the maximum level of around 200 ms (prolonged inhibition). This scenario fits with our data expressing increased masking effect for set-size 6 condition reaching its maximum around 200 ms of SOA. Moreover, depending on the suggestions that NMDA and AMPA receptors are the main resource of feedforward and feedback signaling, respectively; one can infer that mask-originated feedback signal is transmitted through AMPA receptors and target-originated feedforward activity is represented by NMDA receptors. These hypotheses do not contradict the previous discussion about the assumptions on the RECOD model. These might happen both within the P-pathway and can be manifested as intra-channel

inhibition.

An additional possibility to explain our results on the prolonged inhibition component may be the following. It is indicated in a study that since RF of extra-striate areas is bigger, more than one stimulus falling into an RF causes inhibitory interaction for the corresponding neurons [84]. Maybe in our set-size 6 conditions, stimuli were so close that they fell into the same RF at the higher-level visual areas and caused additional confliction and inhibition in that condition.

Another crucial component of the paracontrast masking is facilitation which increases the target visibility in contrast to the other two components. The facilitation component typically becomes dominant in the brightness judgment task which makes sense since brightness processing (filling-in process) is a separate visual process than the contour discrimination (boundary detection) process. Therefore, one can hypothesize that the differential effects of criterion content reflect different/separate neural mechanisms. Supporting these results, we could not observe any facilitation component on our contour discrimination experiment. Hence, we conducted another experiment (see Section 2) using the perceived brightness judgment task under different attentional-load conditions. We also designed several pilot studies to eliminate possible confounding factors. Even though there were observable facilitation and brief inhibition components for the normalized masking data of the set-size 6, as indicated before, we could not find any significant differences between SOA conditions It means that we could not observe a robust facilitation component. We have some critics of this design that are mentioned in the third section. We suspect that the experiment might be too complicated in the phases of adding attentional manipulation to have a robust facilitation component. The facilitation component is claimed to occur as a result of the facilitation/enhancement of the subcortical networks on the cortical processing of the P-pathway (see Figure 1.23). This suggestion has been supported by several researchers and masking models [45, 8]. Based on the theoretical suggestions, we expected to observe an interaction between attention and facilitation component of the paracontrast, since attention has an important influence on subcortical pathways [72].

One can also evaluate these interactions from a cognitive psychology point of view since both attention and visual masking are known to control information selection from sensory memory to VSTM [30, 3]. However, it is important to note that previous studies based on such a perspective were typically used backward (e.g., metacontrast) masking paradigms [54, 31, 85, 86, 12]. These studies suggest that an after-coming/following mask may erase or interrupt the former information in the system and thus mask decreases the visibility of a target by blocking the information transfer to higher-level memory components (e.g., see [54]). Furthermore, it is proposed that interactions between mask and target in the long SOAs (but not in the short SOAs) might be mediated through attention-masking interaction. Specifically, according to this perspective, the interruption induced by mask on attentional processes which transfer target information to the VSTM is the main underlying process [87]. However, it is still not certain whether these interpretations are specific to backward masking (i.e., positive SOAs) or applies to other masking types.

According to another notion, a stimulus must be attended to and reach consciousness in order to be reported precisely. In other words, conscious information cannot be reported without attention [88]. Lamme [88] further claims that iconic memory corresponds to phenomenal consciousness and short-term memory (and beyond, i.e., LTM) corresponds to access consciousness. A decrease in target visibility due to the paracontrast might be explained as the deficiency in correctly reporting at specific negative SOAs. Hence, it may be inferred that information is deteriorated in the specific ranges of brief and prolonged inhibitions to reach consciousness. This logic may support that the paracontrast may lead to changes in the information transfer from iconic memory to VSTM. Thus, our data may suggest that attention and some of the inhibitory mechanisms (i.e., particularly prolonged inhibition operating at long SOAs) of the paracontrast masking interact at some level between sensory memory and VSTM (i.e., phenomenal consciousness and access consciousness). As it is also indicated in the study by Lamme [88], the recurrent interactions from higher-level visual areas are important for information to reach access consciousness.

Object substitution theory also suggests iterative/reentrant processing

throughout the visual cortex. Di Lollo [89] originally proposes that visual information processes are not one-way (i.e., feedforward). In the hierarchy of visual information processing, the recurrent/reentrant connections also play an important role. Even though he claims that reentrant signals interrupt the processing of a preceding target (i.e., backward masking), it may be also the case for forward/paracontrast masking, since feedback signal of a preceding mask from higher-level areas may interact with the processing of the following target in early-level areas. Hence, it may lead to inhibition in target visibility. Although it is hard to visualize a robust masking and set-size effect in the negative SOA range, the performance values of a four-dot forward masking paradigm were in line with our results here [87] such that increased set-size decreases the masking effect in the short SOAs while increasing the masking effect in the large SOAs. Since we used larger set-sizes, our results have extended those findings and revealed significant effects.

4.2 Future Directions

As mentioned in the previous sub-section, the facilitation component would probably get affected by attentional manipulations since both are suggested to originate from sub-cortical pathways. Studying this relationship through a more elaborate and controlled design will be helpful in this respect. Since our design had some limitations to show a robust facilitation component, the findings did not provide a compelling answer. This is still an important issue since there are controversial findings for the independence of metacontrast masking function from attention [3, 37], and, to best of our knowledge, there is no study on the possible interaction of attention and facilitation component of the paracontrast masking. A further investigation can provide information about the effect of the attention on the sub-cortical regions or their independence between them. A possible study could be an upgraded/developed version of the second experiment. Since there were several blank screens and time intervals between stimuli, our design may include some potential confounds in terms of memory components and the subject's ability to perform the task. Also, in our design, the target and comparison

stimuli were presented at different locations of the visual field (fovea vs. periphery). A more controlled version of this design could be achieved by solving these problems. In what follows, a potentially improved version is described.

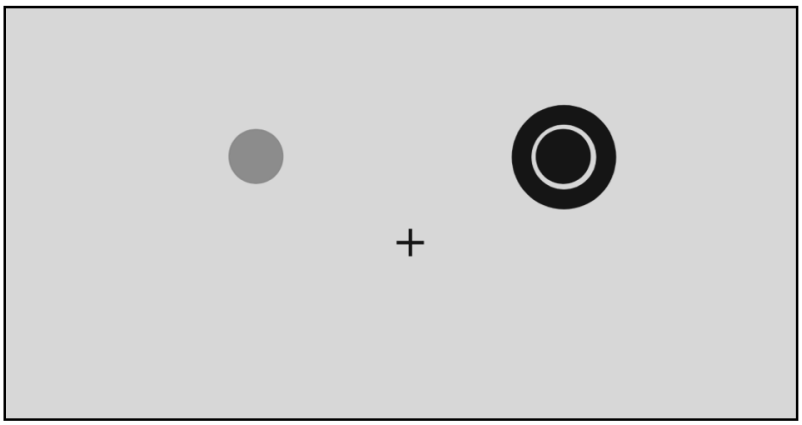

Figure 4.1: The experimental design by Breitmeyer et al. [1] for brightness judgement task leading to robust facilitation component.

In this proposed design, the main starting point is to eliminate the predicted confounds. In the literature, all observations of the facilitation component have been made through a design in which target stimulus and comparison stimulus are typically presented at the same screen, having the same onset-time, and both peripheral (e.g., [1, 2]). The design of a representative former study that causes facilitation is shown in Figure 4.1 Accordingly, such a design can be the origin of set-size 1 (low-attentional load) condition. A proposed design for set-size 1 is presented in Figure 4.2. Here, the stimulus on the right is the target stimulus while the stimulus on the left is the comparison stimulus. The luminance of the comparison is adjusted by the response of a participant performing a brightness judgment task. Since experimental blocks will be repeated several times, the left and right side of the screen (being target or distractor) should be randomized and counterbalanced over repetitions.

For increased set-size conditions, rather than covering up all the screen, the right and left visual fields can be separated for the comparison and target stimuli. In such a design, it would be challenging to have a set-size 6 condition, but it provides a concurrent presentation of comparison and target. Figures 4.3 and 4.4

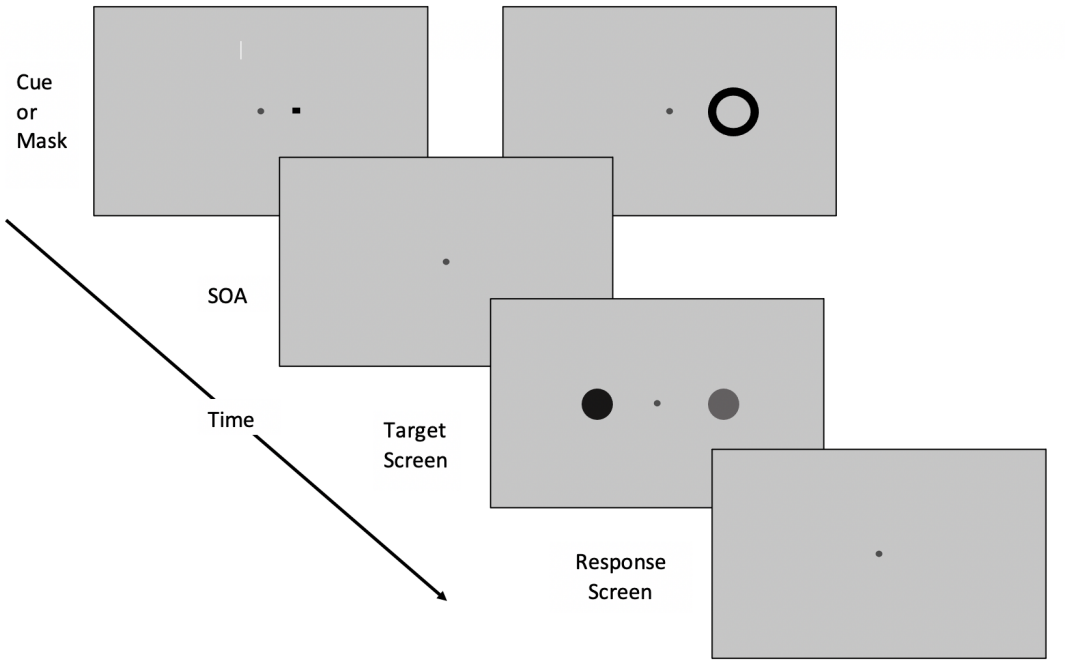

Figure 4.2: Set-size 1 condition of the proposed design. The participants will be instructed to press left or right arrow key representing "target was brighter" or "comparison was brighter", respectively.

show the proposed experimental design for set-size 3 conditions having distractor stimuli at the right or left side, respectively (there are 2 distractors and a target stimulus on one side of the visual field, and a comparison on the other side).

Moreover, an EEG study could be done to further study the relationship between attention and paracontrast and to characterize the temporal dynamics of attention-induced modulations. In a future EEG experiment, the significant alterations in the range of brief and prolonged inhibitions can be examined and the difference between the evoked potentials to masking and baseline cue conditions should be analyzed. Such an EEG experiment will be informative to understand the differential effects of attention on the early and late inhibitory mechanisms in the summed cortical activities.

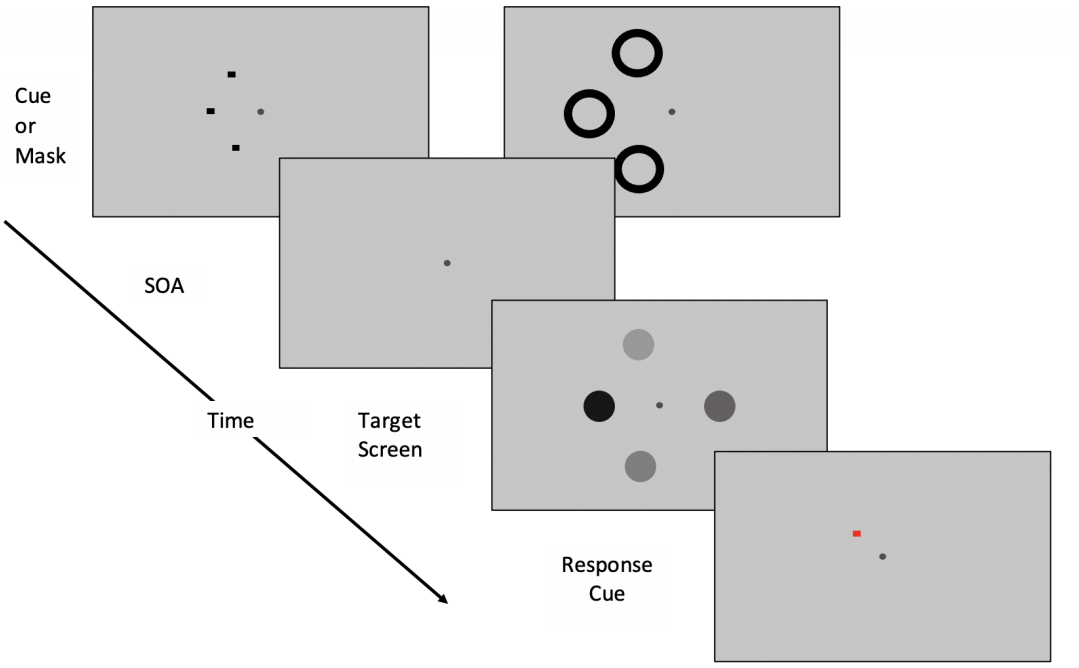

Figure 4.3: Set-size 3 condition for the proposed design. The comparison stimulus will be on the right while target and distractors will be on the left. The location of the target over a set of stimuli on the left is defined by the red response cue. The participants will be instructed to press right or left arrow key representing "target was brighter" or "comparison was brighter", respectively.

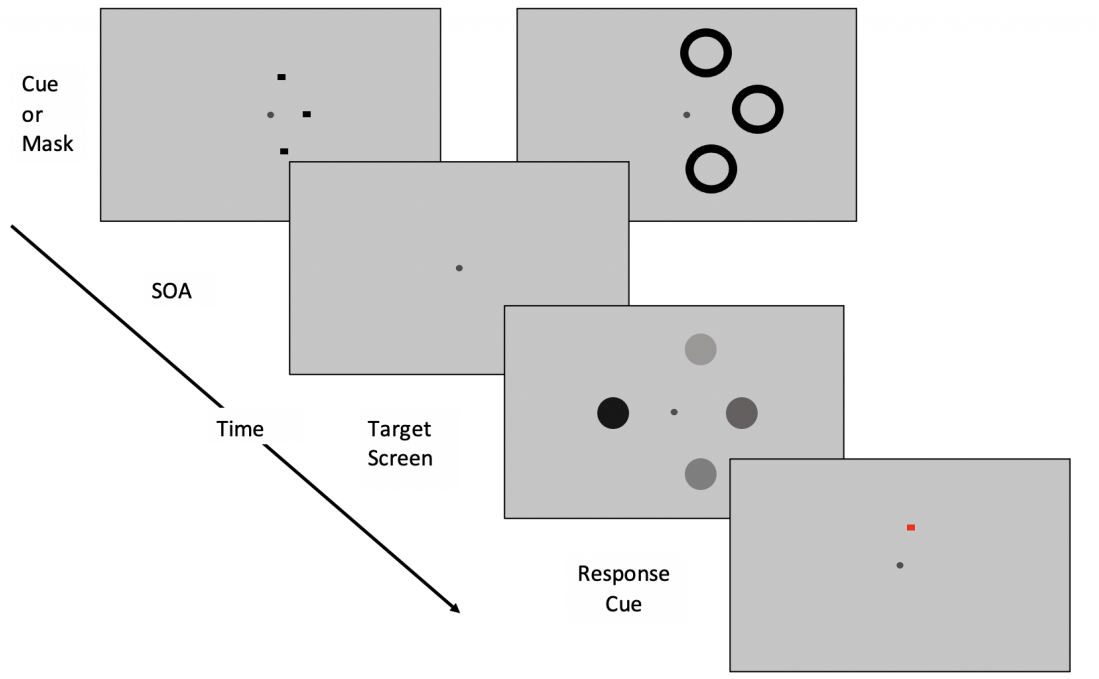

Figure 4.4: Set-size 3 condition for the proposed design. The comparison stimulus will be on the left while target and distractors will be on the right. The location of the target over a set of stimuli on the right is defined by the red response cue. The participants will be instructed to press left or right arrow key representing "target was brighter" or "comparison was brighter", respectively.

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