THE EFFECT OF CONTEXT-DEPENDENT LIGHTNESS ON CONTRAST DETECTION AND IDENTIFICATION, AND ITS NEURAL CORRELATES

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

By
Zahide Pamir Karatok
October 2017

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

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ABSTRACT

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Ph.D. in Neuroscience
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October 2017

Perceived contrast of a grating varies with its background (or mean) luminance: of the two gratings with the same photometric contrast the one on higher luminance background appears to have higher contrast. On the other hand, context often causes a large perceived difference between equiluminant regions (e.g., simultaneous brightness contrast). Does perceived contrast also vary with context-dependent background lightness even when the luminance remains constant? In this study, the effect of context-dependent lightness on contrast perception was investigated using psychophysical and functional magnetic resonance imaging (fMRI) methods. First, we measured appearance judgments of participants and demonstrated that context-dependent lightness of background influences the perceived contrast of rectified gratings. Perceived contrast of gratings superimposed on equiluminant but perceptually lighter background is higher compared to ones on perceptually darker backgrounds. However, this pattern is valid only for incremental, not for decremental contrast.

Literature indicates a significant difference between visual processing near and above threshold. Also, behaviorally it has been shown that appearance and threshold tasks are mediated by different mechanisms. Therefore, here, we also measured the effect of context-dependent lightness on contrast detection and discrimination thresholds using a 2-IFC procedure. Results indicate that both detection and discrimination thresholds are lower for the gratings superimposed on perceptually lighter backgrounds. Differently from the appearance results, the effect was observed both for incremental and decremental contrast.

In an fMRI study, we investigated whether activity in any brain region correlates with background-lightness-dependent contrast perception. Although our stimulus was physically identical, we observed difference in BOLD response within pre-defined region of interests (ROIs) in different visual areas. Both for incremental and decremental contrast, activation, especially in V1, was greater when the grating was superimposed on lighter background for all the contrast levels tested. Variation in V1 activity with varying contrast links better with the detection and discrimination thresholds than the appearance results. Therefore, this study might offer a neural evidence for dissociation between the mechanisms underlying detection (threshold) and identification (appearance) measures. However, the relationship between the threshold and fMRI data does not really agree with the previous findings in literature. These results indicate that the neural activation caused by the detection mechanism may change depending on the absolute or perceived value of the contrast.

Keywords: Contrast, lightness, context, detection, identification, threshold, appearance.

ÖZET

BAĞLAMA DAYALI AÇIKLIĞIN KONTRAST SAPTAMA VE TANIMLAMA ÜZERİNDEKİ ETKİSİ VE BU ETKİNİN NÖRAL KORELASYONLARI

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Nörobilim, Doktora
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Basit bir görsel uyaranın algılanan kontrastı, üzerinde bulunduğu fonun luminansına (veya ortalama luminansa) bağlı olarak değişir. Fiziksel olarak eşit kontrasta sahip iki uyarandan yüksek luminanslı fonda gösterilen uyaranın kontrastı daha yüksek algılanmaktadır. Bir diğer yandan, bağlam sıklıkla luminansı eşit uyaranların algılanan değerlerinin (örneğin açıklık) farklı olmasına sebep olur (eş zamanlı parlaklık kontrastı uyaranı gibi). Bu bilgiler algılanan kontrastın fonun luminansı sabit tutulduğunda bağlamın etkisiyle değişen açıklık değerine bağlı olarak değişip değişmeyeceği sorusunu doğurmaktadır. Bu soruyu yanıtlamak amacıyla, bu çalışmada, psikofizik ve fonksiyonel manyetik rezonans görüntüleme (fMRG) yöntemleri kullanılarak, bağlama dayalı açıklığın kontrast algısı üzerindeki etkisi araştırılmıştır. Bunun için ilk olarak bağlama dayalı açıklığın algılanan kontrastı nasıl etkilediği ölçülmüş ve bir kontrast barının algılanan kontrastının üzerinde bulunduğu fonun açıklık değerinden etkilendiği gösterilmiştir. Buna göre, fiziksel olarak tamamen birbirinin aynı olmalarına karşın, açıklık değeri yüksek olan fon üzerindeki barın kontrastı daha yüksek olarak değerlendirilmiştir. Sonuçlara göre, görsel sistemin açıklık değerini algılanan kontrast değerinin hesaplanmasında kullandığı görülmüştür. Fakat bu etki, sadece luminansı artan kontrast barları (pozitif kontrast) kullanıldığında görülmüş; luminansı azalan kontrast barları (negatif kontrast) kullanıldığında ise kaybolmuştur.

Literatürde, bir uyaranın algılanan değerinin ve eşik değerinin farklı mekanizmalar tarafından belirlendiğine dair bulgular mevcuttur. Bu nedenle, bu çalışmada ayrıca bağlama dayalı açıklığın kontrast saptama ve ayırsama eşiğini nasıl etkilediği uyumsal iki aralıklı zorunlu seçim yöntemi kullanılarak araştırılmıştır. Sonuçlar, kontrast barlarının açıklığı yüksek olan fon üzerine yerleştirildiğinde açıklığı düşük olan fon üzerine yerleştirilmelerine kıyasla sezim ve ayırsama eşiğinin daha düşük olduğunu göstermiştir. Algılanan kontrast deneylerinden farklı olarak burada hem pozitif hem negatif kontrast barları bağlama dayalı açıklıktan etkilenmiştir.

fMRG çalışmasında, beyindeki nöral aktivasyonun bağlama dayalı açıklık etkisini yansıtıp yansıtmadığı araştırılmıştır. Gösterilen fon ve kontrast barları fiziksel olarak tamamen birbirinin aynı olmasına karşın görsel alanlarda önceden belirlenmiş ilgi bölgeleri içinde bu uyaranlara verilen tepki farklılık göstermiştir. Buna göre, özellikle V1 bölgesinde, test edilen tüm kontrast değerleri için kontrast barlarının, açıklığı daha yüksek olan fonlara yerleştirildiği durumda daha yüksek BOLD aktivasyonuna sebep olduğu gözlenmiştir. V1'deki aktivasyon değişimi algılanan kontrast değerlerine kıyasla eşik değerleriyle daha uyumludur. Bu nedenle, bu çalışmanın saptama ve tanımlama görevlerinin farklı mekanizmalar tarafından yürütüldüğüne dair nöral bir kanıt olduğu düşünülmektedir. Fakat, bu çalışmadaki eşik ile fMRI verileri arasındaki ilişki, literatürdeki daha önceki bulgularla tam olarak uyumlu değildir. Bu sonuçlar saptama mekanizmasının yarattığı nöral aktivasyonun kontrastın mutlak veya algılanan değerlerine bağlı olarak da değişebileceği sonucuna işaret etmektedir.

Anahtar sözcükler: Kontrast, açıklık, saptama, tanımlama, eşik, görünüm.

Acknowledgement

I am grateful to many people who made this thesis possible. First of all, I would like to express my deepest appreciation to my advisor Hüseyin Boyacı for his precious support and guidance in all aspects of my graduate studies. It was a priceless opportunity for me to be able to work with him and to learn from him. He has always made me feel that he believes in me and this has kept me motivated throughout this challenging journey.

I would like to thank to Hulusi Kafalıgönül not only for his valuable time and comments on this thesis but also for always being there whenever I need advise that extends beyond my Ph.D. studies. I appreciate all the wisdom and experiences he shared with me.

I would also like to thank to Miri Besken for her critical comments and discussions throughout the thesis progress committees; and to the other jury members Cengiz Acartürk and Didem Kadıhasanoğlu for allocating their valuable times to read and comment on this thesis.

I would like to thank to my dear friend Buse Merve Ürgen for making UMRAM more than a work place for me. I am grateful for her companionship, endless support, and intellectual comments on my studies. I want to thank to Emre Kale for helping me whenever I felt desperate on technical issues. I also want to thank to all other friends in UMRAM for their friendship, good memories, and their support in my studies.

I am grateful to my family for their continuous and unconditional support. Finally, I would like to express my warm gratitude to my beloved husband Mustafa Karatok for sharing all the burden and happiness with me. I feel privileged to have him in my life, and to be embraced by his love and support.

I want to acknowledge The Scientific and Technological Research Council of Turkey (TUBİTAK) for supporting me through BiDEB (2211-E) scholarship, and this study through 1001 Grant (funding ID: 113K210 and 116K380).

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Chapter 1

Introduction

1.1 Background

Visual information processing begins in the retina by detection of visible light [e.g., 1, 2, 3, 4]. Light reflected from the visual world is transduced into neural activity by photoreceptors, rods and cones, and transmitted to retinal ganglion cells in the retina [2, 3]. Because of the center-surround receptive field organization of the retinal ganglion cells, they respond antagonistically to a stimulation in their center and surround region. For instance, for an ON-center OFF-surround neuron, increased luminance at the center increases its response, but increased luminance at the surround decreases it. Therefore, a visual neuron responds weakly to uniform illumination of whole receptive field and it responds strongly when the light intensities in the center and surround are quite different [1, 2, 3, 4]. Hence, the output of retina is not a faithful reproduction of light that reaches the eye from the external world. Instead, it is mostly the contrasts in light [1, 5, 6].[1]

The sensitivity of the retina to the contrast of an image rather than its absolute

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[1] Vision scientists define contrast as a difference in light intensity between dark and light regions of a visual stimulus; or a measure of differences in luminance between light and dark regions compared to the mean luminance in an image [e.g., 7, 8] and calculate the local contrast in an image using various formulas, such as those of Michelson or Weber contrast.

amount of light is not a defect of the visual system. On the contrary, this is what makes the visual system so robust and reliable. The absolute amount of light detected by retina is primarily determined by the intensity of light source such that increasing the ambient light intensity also increases the amount of light reflected by objects [1]. However, in order to identify a particular visual object as the same object under different viewing conditions, visual system should be able to give a fixed response, independent of light source, to the light reflected from that object. The absolute amount of light is relatively inadequate to succeed in object identification [1, 9, 10] because of its dependence on light source. On the other hand, contrast information is quite informative because it is mostly preserved despite the changing ambient light intensity. Thus, the center-surround receptive field organization provides an adaptive advantage by eliminating the uninformative information and transmit the most meaningful information to higher levels in the processing [1]. By doing this, the visual system also ensures to preserve the small differences in light intensity. The visual information is slightly distorted in each relay step it is transmitted during the information processing. Therefore, if information about absolute amount of light is directly sent to higher levels, small differences in light intensities might be lost and not detected because of the distortion. In order to minimize this potential lost, the visual system computes contrast in the retina, at the very beginning of the information processing [1]. On the other hand, by now it is well established that the human visual system is not primarily concerned with estimating the physical and optical properties of images formed on the retina. Instead it seems to be more interested in estimating object and scene properties that are critical for the fitness of the organism [see e.g., 11, 12]. Therefore, despite the elaborate computation of contrast in the retina, photometric quantities of contrast computed in the retina do not always capture the relevant perceived qualities in the image [13], For instance, it is well known that perceived contrast of a simple isolated stimulus, such as a grating, is affected by its spatial frequency and background (or mean) luminance, the measure of the intensity of light reflected from a surface, even when its calculated photometric contrast remains the same [e.g., 7, 14, 15, 16, 17, 18].

While how the visual system accomplishes this remarkable feat of estimating

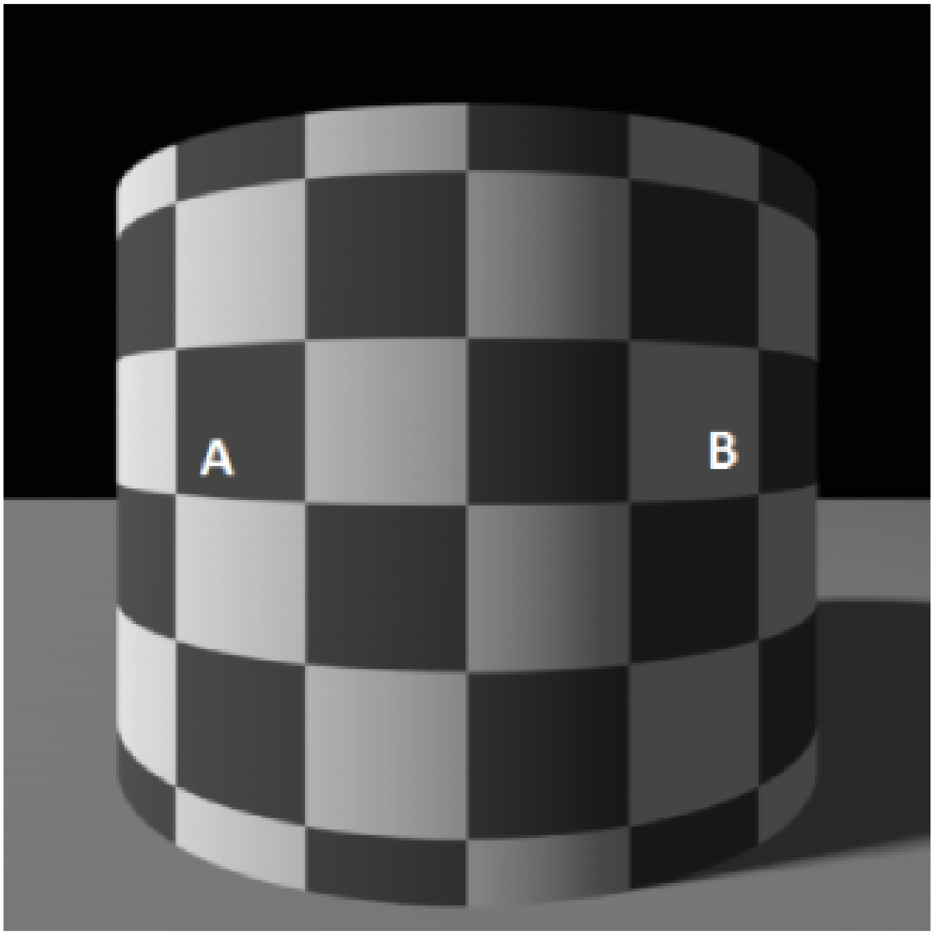

Figure 1.1: Illusory checkerboard stimulus. “Context squares”, A and B have identical luminance but different lightness.

object and scene properties given a pair of inherently ambiguous retinal images is far from being completely understood, it is certain that it uses myriad of contextual cues that are present in a typical everyday scene. For example, in simple configurations luminance and lightness, defined as the perceived relative reflectance, covary. However, it is well known that lightness and luminance do not always covary, instead lightness depends on the context within which the surface is viewed. An example can be seen in Figure 1.1 that even though two surfaces marked as A and B (context squares, CSs) are equiluminant, because of their respective contexts, the visual system estimates (correctly) that their lightnesses are different [also see 19, 20, 21, 22, 2].

Considering the discrepancy between luminance and lightness as Figure 1.1 convincingly demonstrates, a new question arises: does perceived contrast of a grating vary with the luminance or lightness of its background? In other words, suppose that we superimpose grating patterns on CSs (see Figure 2.4), what happens to the perceived contrast of those gratings? If contrast perception varies only with luminance, we would not expect to see any differences in perceived contrast of gratings superimposed on the CSs. Such a result would indicate that unlike other visual features such as luminance [see e.g., 19, 10, 23] or size [see e.g., 24, 25, 26], contrast is largely preserved as it is computed in the retina. Alternatively, contrast might vary with lightness. Then, this would suggest that it is affected by visual context like many other visual features whose computation begins in the retina [see e.g., 19, 10, 23, 24, 25, 26]. The distinction is critical to fully understand the underlying mechanisms of contrast perception. Also, this would help us to understand the visual system better because contrast critically affects visual performance on many tasks such as object identification, speed judgment or motion detection [16]. Moreover, some other features of a visual stimulus such as shape, texture and size are determined via contrast within the object or between the object and background [2]. In addition to these, there is evidence that contrast and luminance are processed via different networks in brain [27, 28, 29, 16]. Therefore, it could also indicate at which level contrast, luminance and lightness operate and interact in the visual system.

Even though context-dependent lightness has been studied extensively [e.g., 30, 31, 32], its effect on perceived contrast was not studied directly and systematically previously. In a number of studies, related problems, particularly the effects of context-dependent lightness (and brightness) on luminance discrimination and detection thresholds were addressed [e.g., 33, 9, 34, 35, 31]. Maertens, Wichmann, and Shapley [36] investigated the effect of surrounding context on the lightness of elliptical regions using Adelson's cylinder-and-checkerboard stimulus [37], and Shapley and Reid's stimulus [38]. In both types of context the authors placed elliptical targets on perceived-dark and perceived-light squares which were in fact equiluminant. They found that lightness of ellipses were assimilated, for example the ellipse placed on perceived-lighter square was also perceived lighter. However they did not asses perceived contrast between those ellipses and their background explicitly, in fact they offered models to explain their lightness results based on the photometric contrast values. Therefore, in a series of studies, we aimed to directly examine the effect of context-dependent lightness on contrast perception.

1.2 Scope and Motivation of the Present Study

In order to investigate the effect of context-dependent lightness on contrast perception, we conducted behavioral and fMRI experiments. First, we conducted behavioral experiments in order to investigate how context-dependent lightness affects contrast appearance judgments (i.e. perceived contrast or contrast identification) and contrast detection and discrimination thresholds. In chapter 2, I introduce a study in which we investigate how perceived contrast of a grating is affected by the luminance and context-dependent lightness of its background [39]. We measured the perceived contrast of incremental and decremental rectified square-wave gratings superimposed on equiluminant but perceptually different backgrounds. Our results demonstrated that context-dependent lightness affects the judgments for contrast. More specifically, perceived contrast of gratings superimposed on equiluminant but perceptually lighter backgrounds was higher compared to those superimposed on perceptually darker backgrounds. In this experiment, we examined the appearance of gratings and we published the results [39].

There is converging behavioral and neural evidence in literature that detection and identification are processed at least by partly separate mechanisms in the brain [9, 40, 41]. For instance, Hillis and Brainard [9] previously indicated that although object detection and identification require the processing of luminance pattern in a stimulus, demands of the two tasks are different. Object detection requires to detect differences in luminance between a particular object and adjacent objects whereas object identification requires to give a fixed response across changing viewing conditions. Considering these different demands, they claimed appearance judgment tasks as we did in our previous experiment model the object identification whereas detection and discrimination threshold tasks model the object detection performance. They also showed behaviorally that detection, and identification of incremental elliptical patches in complex scenes similar to ours were mediated by different mechanisms. Besides, literature indicates significant differences between visual processing near threshold and above threshold [42]. Therefore, it is also crucial for us to understand how context-dependent lightness affects detection and discrimination thresholds of contrast gratings. Here, detection threshold refers to the smallest amount of stimulus energy necessary to detect its presence whereas discrimination threshold can be defined as the smallest difference between two stimuli that a person can detect. With this motivation, in the present study we also aim to investigate the effect of context-dependent lightness on contrast thresholds. In Chapter 3 and Chapter 4, studies in which we investigate how context-dependent lightness affects contrast threshold perception are explained in detail. To examine whether context-dependent lightness has an effect on threshold-level contrast perception, we first conducted detection threshold experiments using our illusory checkerboard stimulus (see Chapter 3). The checkerboard we used in our studies has a strong illusory effect. Therefore, we also tested a weaker illusory lightness stimulus, i.e. the simultaneous brightness contrast (SBC, see an example in Figure 4.1) because we predicted that the effect will correlate with the strength of the illusory lightness effect (see Chapter 4). In these experiments we tested incremental and decremental contrast types, and different frequency levels.

In this study, we also aim to systematically investigate the neural correlates of the context-dependent lightness effect on perceived contrast and contrast thresholds using functional magnetic resonance imaging (fMRI) techniques in order to unveil the underlying neural mechanisms of the context-dependent lightness effect. In Chapter 5 and Chapter 6, fMRI studies are explained in detail. First, an fMRI experiment is conducted in order to examine the effect of context-dependent lightness on associated cortical activity (see Chapter 5). In this study, an interesting relationship between the fMRI, contrast appearance and contrast threshold results was observed. In order to investigate this relationship systematically and to link behavioral and neural data better, we conducted additional behavioral and fMRI experiments of contrast detection and discrimination (see Chapter 6). Results of this study offer a neural evidence for dissociation between the mechanisms underlying detection and identification measures.

Chapter 2

Perceived Contrast in Context

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Measurement of the lightness experiment in Section 2.2 is previously reported in a master's thesis titled "The effect of context luminance on contrast perception" and submitted to the Graduate School of Informatics Institute of Middle East Technical University in August, 2014 by Zahide Pamir. The same data is also reported here in order to show that the illusory checkerboard stimulus used in the present experiments ensures the desired lightness effect. Data for the other experiments in this dissertation is collected especially for this Ph.D. study using the optimal experimental design and parameters decided upon the results of experiments conducted for the above-mentioned master's thesis.

2.1 Introduction

In this study, we investigated the effect of context-dependent lightness on perceived contrast using a stimulus inspired by Adelson's checkerboard stimulus [37].

There were two equiluminant context squares (CSs) on the stimulus, lightnesses of which appeared considerably different (Figure 2.1). This stimulus allowed us to keep the luminance constant and test only the effect of context-dependent lightness.

We conducted two series of experiments in the study. Firstly, we assessed the lightness effect in the stimulus after applying several image manipulations (see Figure 2.1). In the second experiment we measured the perceived contrast of rectified square-wave gratings superimposed on the CSs (see Figure 2.4). Using rectified gratings allowed us to study positive and negative contrast patterns independently, which was critical because both behavioral and neural evidence in previous studies suggest fundamental differences between processing of incremental and decremental luminance patterns [e.g., 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53]. Previous studies in literature have found interactions between spatial frequency and mean luminance in contrast perception using simple gratings [54, 14, 55, 15, 56]. More specifically, perceived contrast of high-frequency gratings were more strongly affected by the mean luminance [15]. Therefore, in our experiments we included spatial frequency as a further condition. Besides, additional control experiments were conducted to address possible confounds and the effect of actual changes in luminance. Detailed information about the experiments can be found in [39].

2.2 Measurement of the Lightness Effect

In this experiment, we quantified the lightness effect in the illusory checkerboard stimulus after several image manipulations in order to ensure that there is a significant lightness effect in our stimulus. The lightness effect is defined and quantified as the difference between the lightnesses of the CSs marked “A” and “B” in Figure 2.1. Also, the other purpose of this experiment was to find the impact of image manipulations on the strength of the lightness effect. This allowed us to identify the stimuli with strong lightness effects to use in subsequent contrast experiments.

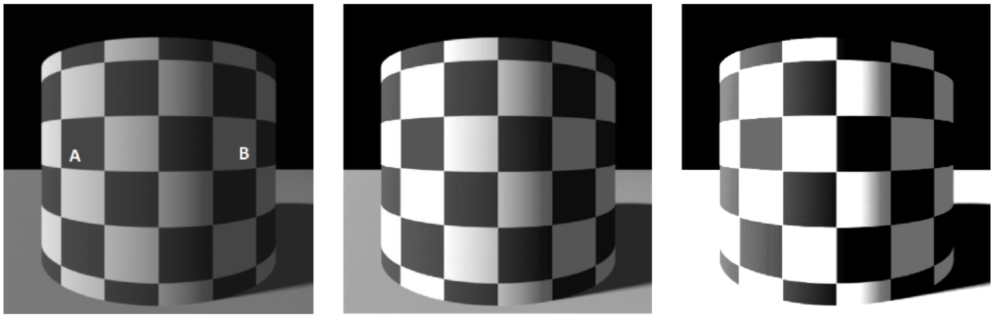

Figure 2.1: Examples of the stimulus after image manipulations. “Context squares” (CSs), A and B in the first image and in the same position in all images, have identical luminance but different lightness.

2.2.1 Methods

2.2.1.1 Participants

Eight participants (three male) including the author ZP participated in the experiment. The mean age was approximately 23.4 ranging from 21 to 26. All participants reported normal or corrected-to-normal vision, and had no history of neurological or visual disorders. Participants gave their written informed consent and the experimental protocols were approved by the Human Ethics Committee of Bilkent University.

2.2.1.2 Stimuli and Design

The experimental software was prepared by us using the Java programming platform. The stimuli were presented on a CRT monitor (HP P1230, 22 inch, 1600×1200 resolution). Presentation of correct luminance values was ensured by using a gray scale look-up table prepared after direct measurements with a colorimeter (SpectroCAL, Cambridge Research Systems Ltd., UK). Participants were seated 75 cm from the monitor, and their heads were stabilized using a chin rest. Participants’ responses were collected via a standard computer keyboard.

A variant of Adelson’s checkerboard stimulus (“illusory checkerboard stimulus”

Figure 2.2: Lightness experiment. Participants' task was to adjust the luminance of an external patch to match the lightness of the context squares. The matching patch was placed on a random-noise background. Instructions about which context square is tested in that particular trial was given by the text strings "LEFT" and "RIGHT" on the random-noise background. The arrow and the text "adjustable patch" were not shown on the screen during the experiment.

or "stimulus" from here on, Figure 2.1) was generated using the open source rendering package Radiance [57]. The stimulus subtended 9.5 by 9.5 degrees of visual angle. Approximate size of the CSs was 0.85 by 0.85 degrees of visual angle. We prepared eleven different versions of the stimulus by manipulating the overall image contrast and luminance using the open-source software GIMP (http://www.gimp.org/). After these image manipulations, luminance of the context squares were 1.64, 2.74, 2.86, 4.34, 6.58, 10.1, 12.65, 16.11, 17.4, 20.41 and 26.15 cd/m^2 (mean luminance of the stimulus: 1.83, 3.9, 5.13, 5.83, 6.98, 11.34, 13.18, 16.43, 16.74, 21.14, 23.37 cd/m^2, respectively). Because of the configuration of the stimulus the right CS was subjectively lighter than the left one (see Figure 2.1 for examples).

Participants' task was to adjust the luminance of an external patch until its lightness matched that of the CSs. The matching patch was placed on a random-noise background, subtending 15 × 3 degrees of visual angle (Figure 2.2). Luminance of each pixel on the random-noise background was drawn from a random distribution between 0 and maximum possible luminance of 100.32 cd/m^2, and the resulting image was convolved with a 6-by-6 uniform filtering kernel. The size of the matching patch was approximately the same as that of the CSs. The initial luminance of the matching patch was determined randomly at the beginning of each trial. Adjustments could be done in large steps (approximately 2 cd/m^2) using the right and left arrow keys or in smaller steps (approximately 0.2 cd/m^2) using the up and down arrow keys. Instructions about which CS is tested in that particular trial was given by the text strings "left" and "right" on the random-noise background. Each variant of the stimulus was presented five times for each context square. This resulted in 110 trials completed in one experimental session (11 stimulus versions (CS luminance levels) × 2 CS positions × 5 repetitions). The order of trials was randomized.

2.2.1.3 Data Analysis

Data were analyzed using SPSS Version 19 (SPSS Inc., Chicago, IL). A repeated measures analysis of variance (ANOVA), was conducted in order to test two factors: CS luminance (11 levels), and CS position (two levels: left, right). Additionally, the magnitude of the lightness effect, quantified as the difference between right and left CS settings, was tested with two-tailed paired-samples Student's t-test for each level of CS luminance.

2.2.2 Results

Figure 2.3 shows the deviation of the raw settings from the actual CS luminances. Analyses showed that main effect of CS position was statistically significant ($F(1,7) = 89.8$, $p < 0.001$). Mean deviation from the actual luminance for

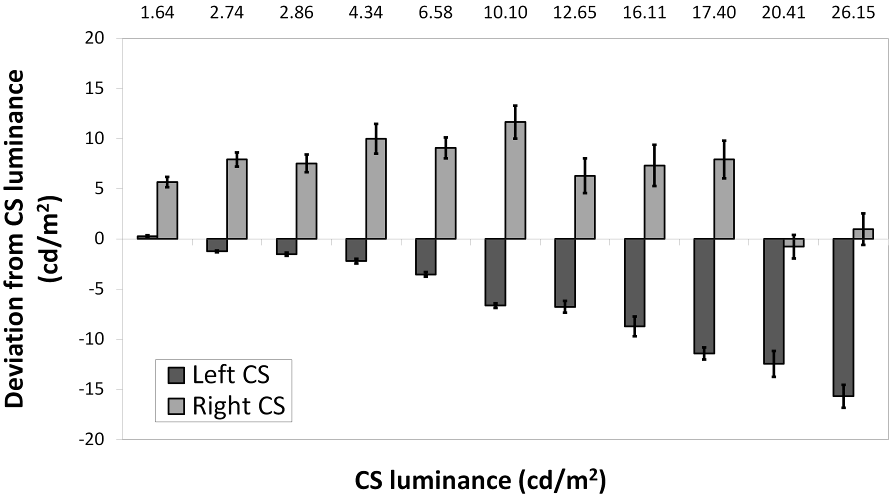

Figure 2.3: Results of the lightness experiment. Deviation of settings from actual luminance is plotted for each CS position as a function of context square luminance. Positive (negative) deviation means setting was higher (lower) than the actual CS luminance. A value of "0" corresponds to perfect luminance match. Under all conditions, participants judged the right CS statistically significantly lighter, consistent with the subjective experience in Figure 1.1. Error bars show ±1 SEM.

the right CS (M = 6.68, SEM = 1.18) was higher than that for the left CS (M = -6,36, SEM = 0.37). Two-tailed paired-samples Student's t-test results showed that settings for left CS and right CS were statistically significantly different at all luminance levels tested (among 11 conditions: minimum t(7)=6.37; maximum t(7)=13.3; mean t(7)=9.03; $p < 0.001$ for all conditions). These results clearly show that, even though the CSs were equiluminant the right CS was perceived lighter, which is consistent with the subjective experience in Figure 2.1. In addition, we found a main effect of the context square luminance (F(10,70)=59.06, $p < 0.001$): as the luminance of context squares increased the lightness effect tended to increase.

2.2.3 Intermediate Summary and Discussion

In all conditions tested we found a significant effect of context on lightness, which slightly increased with CS luminance. Thus the lightness effect in our stimulus was so robust that we could utilize it to test the effect of context-dependent lightness on contrast perception. Because there was not a big difference in the lightness effect across different CS luminance values, we used four versions of the context stimulus in the following contrast experiments: one with a high, one with a medium, and two with low CS luminances. We included two low CS luminances because results of Peli and his colleagues [7] suggest that the effect of mean luminance on perceived contrast is stronger for lower luminances.

2.3 Measurement of Perceived Contrast

In this experiment, we investigated the relationship between context-dependent lightness and perceived contrast. For this purpose, we used rectified gratings superimposed on CSs with positive contrast (incremental grating, i.e., luminance of grating's bars is higher than the background), and negative contrast (decremental grating, i.e., luminance of grating's bars is lower than the background) (see Figure 2.4). We tested four versions of the illusory checkerboard stimulus that led to strong lightness effects based on the results of the first experiment. We compared the perceived contrast of photometrically identical incremental and decremental gratings superimposed on equiluminant but perceptually different CSs (Figure 2.4).

2.3.1 Methods

2.3.1.1 Participants

Incremental grating condition. Two males and four females participated in the experiment under the incremental grating condition. Two of them were among the participants of the lightness experiment and they also participated in the experiment under the decremental grating condition. The mean age was 24.6 ranging from 22 to 29.

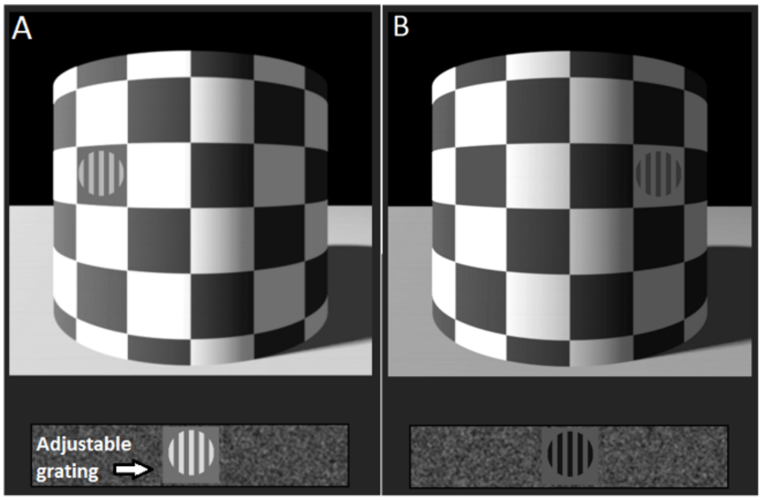

Figure 2.4: Task and procedure in the contrast experiment. Participants were asked to adjust the contrast of a "match" grating to match that of the "standard". Standard was always placed on one of the CSs. The match was placed on a square, which was placed on a random-noise background. The arrow, and the text "adjustable grating" were not shown on the screen during the experiment. (A) Incremental grating condition, (B) decremental grating condition.

Decremental grating condition. Two males and four females participated in the experiment under the decremental grating condition. Two of them were among the participants of the lightness experiment and they also participated in the experiment under the incremental grating condition. The mean age was 25.3 ranging from 23 to 28.

All participants reported normal or corrected-to-normal vision, and had no history of neurological or visual disorders. Participants gave their written informed consent and the experimental procedures and protocols were approved by the Human Ethics Committee of Bilkent University.

2.3.1.2 Stimuli and Design

The contextual stimulus and the physical components of the experimental setup were the same as in the lightness experiment, except a bigger version of the context stimulus was used (13.4 by 13.4 degrees visual angle).

We estimated the perceived contrast of incremental and decremental rectified square-wave gratings superimposed on the CSs (Figure 2.4). Our aim was to compare the perceived contrast of photometrically identical gratings superimposed on equiluminant but perceptually different CSs. Participants' task was to perceptually adjust the contrast of a "match" grating to match that of the "standard" grating. The standard was always placed on one of the CSs. The match grating was placed on a square that had the same luminance and approximately the same dimensions as the CS, which in turn was placed on an external random-noise background (Figure 2.4). Contrast of the gratings was defined by Weber Contrast, $C = (L_{gr} - L_{CS})/L_{CS}$, where L_{gr} and L_{CS} correspond to grating and CS luminance respectively [58]. The positive contrasts tested were 0.1, 0.3 and 0.6, and the negative contrasts were -0.1, -0.3 and -0.6. Adjustment was done in $\Delta C = 0.1$ steps by the use of left and right arrow keys and fine tuned adjustment was done in $\Delta C = 0.01$ steps using the up and down arrow keys. Four versions of the context stimulus were used, in which CS luminances (background luminance) were 1.64, 2.86, 10.1, and 17.4 cd/m^2. Stimuli were presented in a random order on a black background. Gratings with frequencies of 2.5, 5, and 10 cycles/degree (cpd) were tested, blocked in different sessions. Match always had the same frequency as the standard. In each trial the contrast of the standard was pseudo-randomly chosen among the contrast levels tested and balanced across the session. Match had the same contrast polarity as the standard and its initial contrast was determined randomly at the start of each trial. During the trial the background luminance of the match remained constant and equal to that of the CSs. Thus, when the participants adjusted the contrast of the match grating the mean luminance of match background-plus-grating slightly varied. This may have a very small or negligible effect, which should not change the main conclusions because we always compare the settings for physically identical CSs. Each session contained 120 trials with 5 repetitions for every combination of conditions (4 stimulus versions (CS luminance) $\times$ 3 contrast levels $\times$ 2 CS positions $\times$ 5 repetitions). Different frequency levels are tested in separate sessions.

2.3.1.3 Data Analysis

The analyses were performed on an "effect score" defined by

$$\rho_C = \frac{C_R - C_L}{C_R + C_L}, \tag{2.1}$$

where C_R and C_L stand for the participant's setting for the grating superimposed on the right and left CS respectively. An effect score of zero would mean no difference in perceived contrast between the gratings. For decremental contrasts, before computing ρ_C we first converted the contrast settings to positive values (therefore a positive ρ_C means perceived contrast on the right CS is more negative in the case of decremental gratings). In order to test whether the effect score is different than "0" we conducted one-sample two-tailed Student's t-test in SPSS. Effect scores obtained under different contrast types were compared using a two-tailed independent-samples t-test in SPSS. Further analyses were conducted using a repeated measures ANOVA with three factors (luminance, frequency, and contrast) and Bonferroni corrected pairwise comparisons in SPSS.

2.3.2 Results

Results are plotted in Figure 2.5 in the form of effect score. In the incremental grating condition, mean effect score was positive ($\overline{\rho}_C$ = 0.14 SEM = 0.02), and statistically significantly different than zero (t(5) = 8.03, $p < 0.01$). In other words, perceived contrast was higher when the grating was located on the perceptually lighter right CS. In the decremental grating condition mean effect score was negative ($\overline{\rho}_C$ = -0.01, SEM = 0.02). However, it was not statistically significantly different than zero (t(5) = -0.52, $p > 0.05$). In other words, there was no difference between perceived contrast of decremental gratings superimposed on the left and right CS. Effect scores for incremental and decremental gratings were statistically significantly different (t(10) = 5.48, $p < 0.01$). There was no significant main effect of frequency on the results in either condition (incremental grating: F(2,10) = 0.1, $p > 0.05$; decremental grating: F(2,10) = 1.02, $p > 0.05$). Therefore, Figure 2.5 shows the effect scores averaged across frequencies.

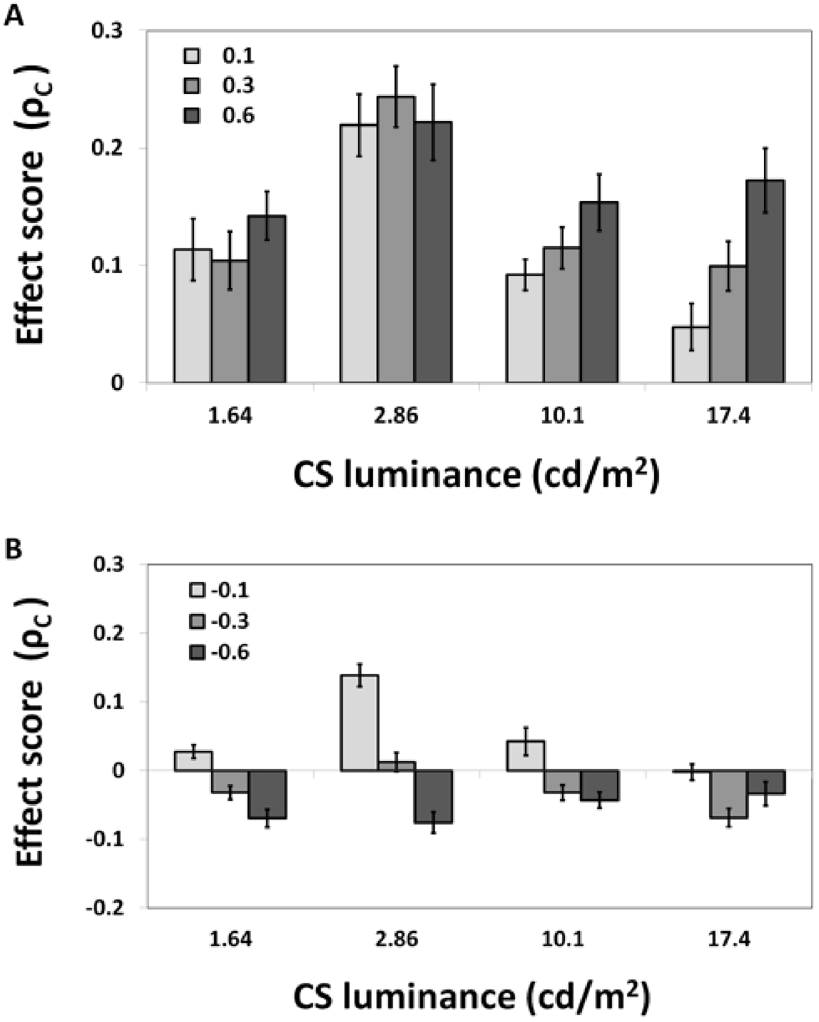

Figure 2.5: Mean effect scores, $\bar{\rho}_C$, from the contrast experiment. Brightness of the bars indicate different contrast levels. Because frequency did not have a main effect, effect scores are averaged over three frequency levels. An effect score of "0" means that there is no difference between perceived contrasts of the gratings superimposed on the right and left CSs. A positive (negative) value means that the absolute value of the perceived contrast of the grating on the lighter CS was greater (less) than that on the darker one. (A) Incremental grating condition. (B) Decremental grating condition. Error bars show ±1 SEM.

CS luminance affected ρ_C in both conditions (incremental grating: (F(3,15) = 10,6, $p < 0.05$; decremental grating: F(3,15) = 6.72, $p < 0.05$). We did not find an effect of standard contrast in the incremental grating condition (F(2,10) = 2,85, $p > 0.05$). However, standard contrast affected ρ_C in the decremental grating condition (F(2,10) = 12.21, $p < 0.05$).

2.3.3 Intermediate Summary and Discussion

Results of this experiment showed that context-dependent lightness affects perceived contrast of an incremental grating: the same grating appears to have higher contrast when it is superimposed on an equiluminant but perceptually lighter background. This result is in line with previous findings, which demonstrated that perceived contrast is higher for gratings with higher mean luminance even when their photometric contrast remains constant [7, 15]. However, interestingly we found no effect of context-dependent lightness for decremental gratings and there was no main effect of spatial frequency.

2.4 Effect of Background Luminance Differences on Perceived Contrast

We conducted an additional experiment in order to directly compare the effects of luminance and context-dependent lightness. In this experiment we measured the perceived contrast of gratings superimposed on a pair of gray-scale patches without the three-dimensional context (see Figure 2.6). Luminances of the isolated patches were different and they were determined based on the group average results of the lightness experiment to approximate the perceptual difference between the CSs. Results are also compared to the findings of [7], where mean or background luminance was shown to have an effect on perceived contrast.

2.4.1 Methods

2.4.1.1 Participants

The same participants (four female, two male) who took part in decremental grating condition in the previous experiment participated in this experiment.

2.4.1.2 Stimuli and Design

In this experiment we measured the perceived contrast of gratings superimposed on a pair of gray-scale patches without the three-dimensional context. Two patches were located at the same spatial positions and dimensions as the CSs in Experiment 2.3. Luminances of the isolated patches were different and they were determined based on the group average results of the lightness experiment (Experiment 2.2) to approximate the perceptual difference between the CSs. More specifically the left patch had a lower and the right patch had a higher luminance. Four pairs of luminances were used, corresponding to the CS luminances of 1.64, 2.86, 10.1, or 17.4 cd/m^2 (note that this is the same set of luminance values used in Experiment 2.3). For example, for the CS luminance of 1.64 cd/m^2, we used 1.92 cd/m^2 for the left and 7.3 cd/m^2 for the right patch, as these were the average settings obtained in the lightness experiment for the left and right CSs respectively. Other luminance pairs were as follows: 1.33, and 10.39 cd/m^2; 3.46, and 21.75 cd/m^2; 5.98, and 25.33 cd/m^2. A match grating was superimposed on a patch with a luminance that corresponded to the tested patches in that trial (1.64, 2.86, 10.1, or 17.4 cd/m^2), which in turn was placed on an external random-noise background. Participants' task was to adjust the contrast of the match grating to match that of the standard grating. The standard grating was pseudo-randomly superimposed on one of the two patches, and its contrast could be 0.1, 0.3, or 0.6 in the incremental grating condition, and -0.1, -0.3, or -0.6 in the decremental grating condition. The initial contrast of the match was determined randomly at the start of each trial. Both match and standard gratings had a spatial frequency of 2.5 cpd. There were 120 trials (4 luminance pairs × 3 contrast levels × 2 patch positions × 5 repetitions) in each session. Participants completed two sessions, one for incremental gratings and one for decremental gratings.

2.4.1.3 Data Analysis

Raw data were converted to effect scores as defined before (see Equation 2.1). For the decremental gratings, before computing ρ_C we first converted the contrast settings to positive values (therefore in case of decremental gratings a positive score means that perceived contrast on the right (higher luminance) patch is more negative). All further analyses were performed on the effect scores. A two-tailed one-sample t-test was conducted to test whether the effect score is different than zero. In order to determine the effect of other factors (luminance pair and contrast), a repeated measures ANOVA was applied. Incremental and decremental grating conditions were compared using two-tailed paired-samples t-tests. Finally, two-tailed independent-samples t-tests (for incremental gratings) and two-tailed paired-samples t-tests (for decremental gratings) were employed to compare the effect scores with those in Experiment 2.3.

2.4.2 Results

Results are shown in Figure 2.6. Under the incremental grating condition the mean effect score was positive ($\overline{\rho}_C$ = 0.2, SEM = 0.03) and statistically significantly different than zero (t(5) = 6.08, $p < 0.01$), which means perceived contrast was higher when the grating is placed on a higher luminance background. However, under the decremental grating condition the mean effect score was not statistically significantly different than zero ($\overline{\rho}_C$ = 0.05, SEM = 0.02; t(5) = 1.93, $p > 0.05$). The difference between the effect scores for incremental and decremental gratings was statistically significant (t(5)=3.07, $p < 0.05$).

Next we compared the results with those from Experiment 2.3. For incremental gratings there was not a significant difference between the effect scores (t(10)=1.23, $p > 0.05$). Overall, effect scores tended to be larger for isolated

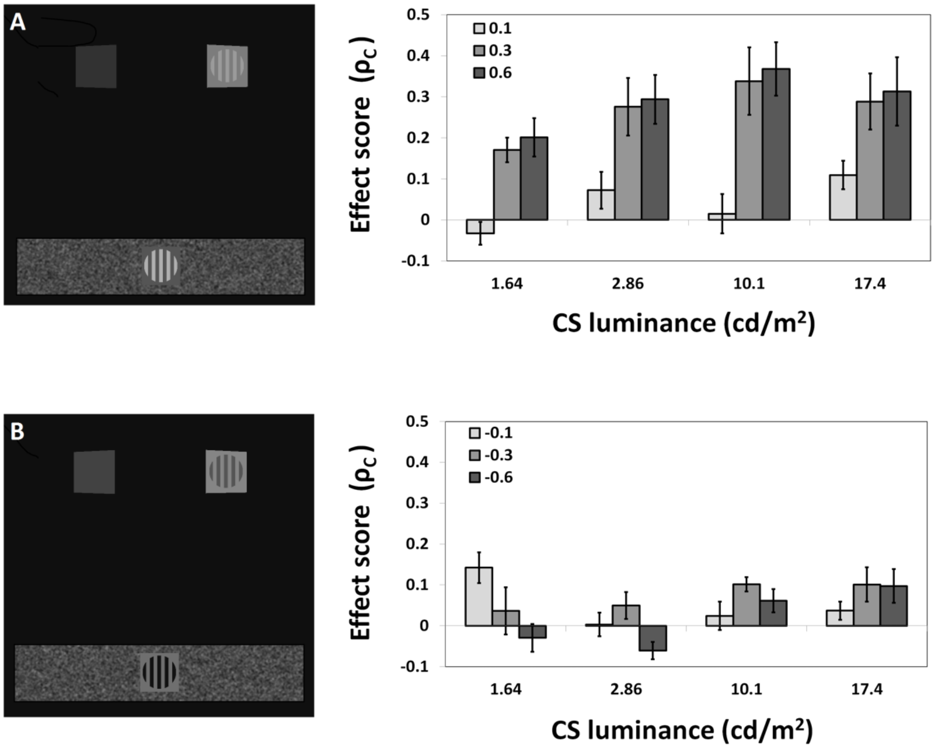

Figure 2.6: Perceived contrast of gratings on isolated backgrounds. Experimental design and results. Participants adjusted the contrast of the match grating to match that of the standard on isolated patches. The geometry and position of the patches were identical to those of the CSs in the contextual stimulus. However this time the patches actually differed in luminance. (A) Incremental gratings. (B) Decremental gratings. The two bar plots on the right show the results presented in the same format as in Figure 2.5. The pattern of results was similar to the one found in Experiment 2.3. Error bars show ±1 SEM.

patches with different luminance (2.5 cpd condition on CSs: $\overline{\rho}_C = 0.15$, SEM = 0.03; on isolated patches: $\overline{\rho}_C = 0.2$, SEM = 0.03). For the decremental gratings the difference was statistically significant (t(5)=2.73, $p < 0.05$; 2.5 cpd condition on CSs: $\overline{\rho}_C$ = -0.02, SEM = 0.03; on isolated patches: $\overline{\rho}_C = 0.05$, SEM=0.02).

2.4.3 Intermediate Summary and Discussion

Results show that background luminance affects perceived contrast of incremental gratings, which is in line with previous literature [e.g., 7]. However, there was no effect of luminance on the perceived contrast of decremental gratings. The pattern of results is consistent with Experiment 2.3, although in general the effect of luminance tends to be larger than that of context-dependent lightness.

2.5 Measurement of Lightness of the Gratings

In Experiment 2.3, where gratings were superimposed on CSs, participants could have used a strategy where they match the lightness of gratings to perform the task, instead of matching their contrast. In order to rule out this possibility and to ensure that participants indeed performed the given contrast task we conducted a control experiment. Here we asked the participants to estimate the lightness of incremental gratings superimposed on CSs in the contextual stimulus. We then used these estimates to calculate "derived contrast" and "derived effect score" as described below. Finally we compared the derived scores to those obtained in Experiment 2.3.

2.5.1 Methods

2.5.1.1 Participants

The same six participants who participated in Experiment 2.3 incremental grating condition completed this experiment.

2.5.1.2 Stimuli and Design

A standard grating with one of 0.1, 0.3, or 0.6 Weber contrast was superimposed on one of the CSs in a pseudo-random order. Participants' task was to adjust the luminance of an external circular matching patch to match the gratings in lightness (*i.e.* the vertical "bars"). The match was placed on a square that had the same luminance as the CS and approximately the same dimensions, which in turn was placed on an external random-noise background (Figure 2.7).

2.5.1.3 Data Analysis

Results from this experiment were converted first to "derived contrast" by placing participants' estimate, $\hat{L}_{gr}$, in the contrast equation, $C = (L_{gr} - L_{CS})/L_{CS}$. Next "derived effect scores" were computed using Equation 2.1, based on the derived contrast values, and compared with the results from Experiment 2 using two-tailed paired-samples Student's t-test.

2.5.2 Results

Results are shown in Figure 2.7. We found that derived effect scores of this experiment and those obtained in Experiment 2.3 were statistically significantly, and extremely different (overall difference: $t(5) = 23.37$, $p < 0.001$). For instance, for the CS with a luminance of 2.86 cd/m^2 and grating with a contrast of 0.3, the

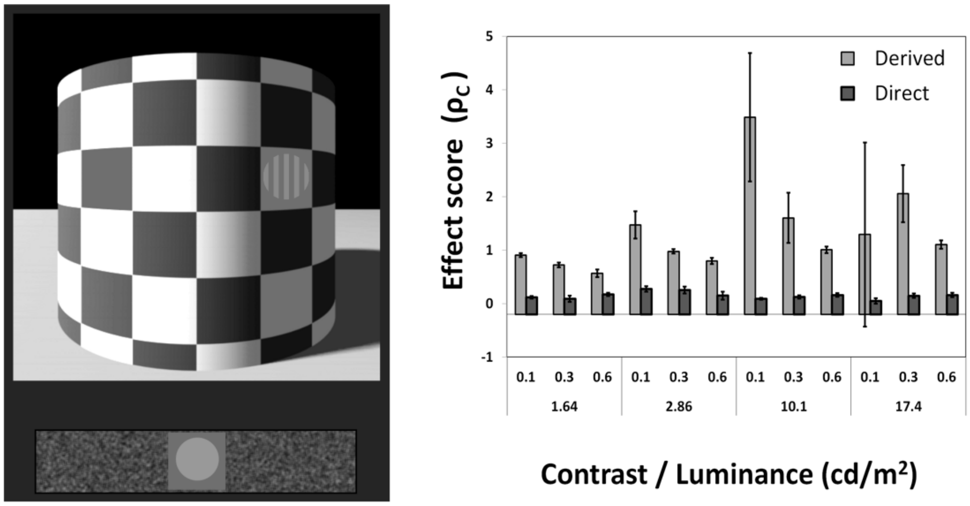

Figure 2.7: Lightness of the gratings. In this experiment participants matched the lightness of the gratings using an external circular match placed on a patch and random noise background. "Derived contrast" and "derived effect score" were computed using those estimates. Derived effect scores and the effect scores from Experiment 2 are shown in the right panel. Clearly, participants performed the two tasks differently. Error bars show ±1 SEM.

effect score was 0.25 in Experiment 2.3, whereas here the derived effect score was 0.97 (Figure 2.7). These results show that if participants were simply matching the lightness of gratings without considering contrast at all, we would obtain extremely different results for the contrast matching experiments. Thus, the results provide a strong evidence that participants matched the contrasts of gratings, not their lightnesses in the contrast experiments.

2.6 Summary and Discussion

Results of this study showed that perceived contrast is not determined solely by the localized features of the retinal image. Context-dependent lightness, as well as actual luminance, of the background influence the perceived contrast of rectified gratings. Our results are consistent with previous studies which showed that perceived contrast of visual patterns in simple scenes, such as Gabor patches on a uniform background vary with their mean or background luminance [e.g., 7, 59, 15]. Additionally, in our study, we showed that this effect is not limited to the background luminance but extends to context-dependent lightness. Moreover, in our study we showed that even when there is no physical difference between the patterns there is still an effect of background lightness on perceived contrast. Comparing physically identical patterns circumvents nonlinearities and confounds that might in principle be introduced by physical changes.

Chapter 3

Contrast Detection Threshold Measurement Using Illusory Checkerboard Stimulus

In our previous study (Chapter 2), we examined the appearance of gratings and we showed that context-dependent lightness affects perceived contrast. In other words, context affects the appearance of contrast gratings. But the function of the visual system is not limited to appearance judgments, it also includes discrimination and detection. Moreover, appearance, and discrimination and detection could be mediated by distinct neuronal mechanisms [9]. Therefore, appearance and threshold performance might be affected differently by context-dependent lightness. To investigate this possibility, we measured the effect of context-dependent lightness on contrast detection threshold using the illusory checkerboard stimulus introduced in previous chapters. In this experiment, we tested incremental and decremental contrast types, and different frequency levels. Also, in a pilot experiment, we tested only incremental gratings and could see the effect on detection thresholds. Details of the pilot experiment can be found in Appendix A.

3.1 Methods

3.1.1 Participants

Five participants (one male) including author ZP participated in the experiment. The mean age was approximately 27 ranging from 23 to 29. All participants reported normal or corrected-to-normal vision, and had no history of neurological or visual disorders. Participants provided written informed consent and the experimental protocols were approved by the Human Ethics Committee of Bilkent University.

3.1.2 Stimuli and Design

The experimental software was prepared using the Java programming platform (http://hboyaci.bilkent.edu.tr/PsychWithJava/). The stimuli were presented on a CRT monitor (HP P1230, 22 inch, 1024 X 768 resolution). To be able to present very fine-grained contrast differences, the dynamic luminance range of the monitor is increased (14-bit luminance resolution) using a digital-to-analog converter (Bits#, Cambridge Research Systems Ltd., UK). Presentation of correct luminance values was ensured by using a 14-bit gamma-corrected gray scale lookup table prepared after direct measurements with a colorimeter (SpectroCAL,Cambridge Research Systems Ltd., UK). Participants were seated 60 cm from the monitor, and their heads were stabilized using a chin rest. Participants' responses were collected via a standard computer keyboard.

Illusory checkerboard stimulus subtended 13.4 by 13.4 degrees visual angle. Approximate size of the context squares (CSs) was 1.2 by 1.2 degrees of visual angle. Rectified square-wave gratings weighted by two-dimensional isotropic Gaussian envelopes were superimposed on the context squares of the illusory stimulus. Gratings with frequencies of 2, and 4 cpd were tested, blocked in different sessions. Luminance of the context square was 10.1 cd/m^2 (Mean image luminance was 11.34 cd/m^2). Gratings with incremental and decremental contrast

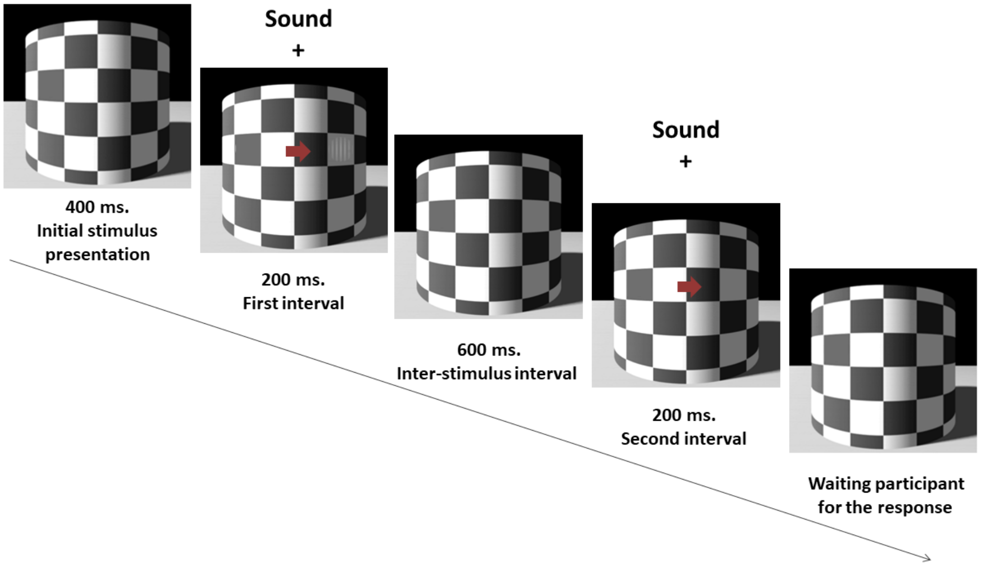

Figure 3.1: Protocol for the detection threshold experiment. At the beginning of each trial, either original checkerboard stimulus or the mirror-symmetric version of it was presented randomly. An arrow was used to inform participants about the side of the stimulus on which the grating would be presented. Gratings were superimposed on only one of the CSs, either darker or lighter, throughout a session. In each trial, a grating is presented at one of the intervals selected randomly. Participants are asked to decide in which interval the grating is presented. Participants are allowed to look at the target CS directly.

were tested in different sessions.

In the experiment, detection thresholds were estimated using an adaptive two-interval forced-choice (2-IFC) procedure (Figure 3.1). At the beginning of each trial, either original checkerboard stimulus or the mirror-symmetric version of it presented randomly. An arrow was used to inform participants about the side of the stimulus on which the grating would be presented. Gratings were superimposed on only one of the CSs, either darker or lighter, throughout a session. Each trial started with a 400-millisecond (ms) illusory stimulus presentation, followed by two intervals each presented for 200 ms. Intervals were separated by a 600-ms inter-stimulus interval (ISI), the illusory stimulus remained on the screen during the ISI. A beep-sound was presented at the beginning of each interval in order to inform participants that the interval begins. The grating was randomly presented at one of the intervals and participants were allowed to look at the target CS directly. Participants were asked to decide the temporal position of the grating. Two interleaved staircases with a starting point 0.002 and 0.02 contrast level (80 trials each, 160 trials in total) were applied in a single session. After each trial, contrast of the next grating was decided based on the previous responses following a 1-up 3-down adaptive staircase with 0.001 contrast steps. The contrast of the grating was decreased one step (makes the task harder) following three consecutive correct answers, and increased one step following an incorrect answer. There was no time constraint; the illusory checkerboard stimulus remained on the screen until the participant gave a response. Observers participated in eight experimental sessions (2 CSs (darker or lighter) X 2 contrast type (incremental or decremental) X 2 frequency levels (2 or 4 cpd)).

3.1.3 Data Analysis

Data were first analyzed with Palamedes toolbox [60] to find the detection threshold (79% success) in Matlab (R2016b, MathWorks). A psychometric function (PF) was fit to the raw data with a Weibull function and lapse rate was fixed to 0. Standard error of the thresholds were calculated for each participant using bootstrapping. Mean thresholds averaged across observers and standard error of mean for each condition were computed and plotted in figures. For decremental contrasts, before computing the threshold, we first converted the levels to positive values.

We conducted ANOVA on the estimated threshold values with three factors (contrast type, CS, frequency). Further, thresholds for different CSs obtained under different contrast types were averaged over two frequency levels and compared using a two-tailed paired-samples Student's t-test in SPSS.

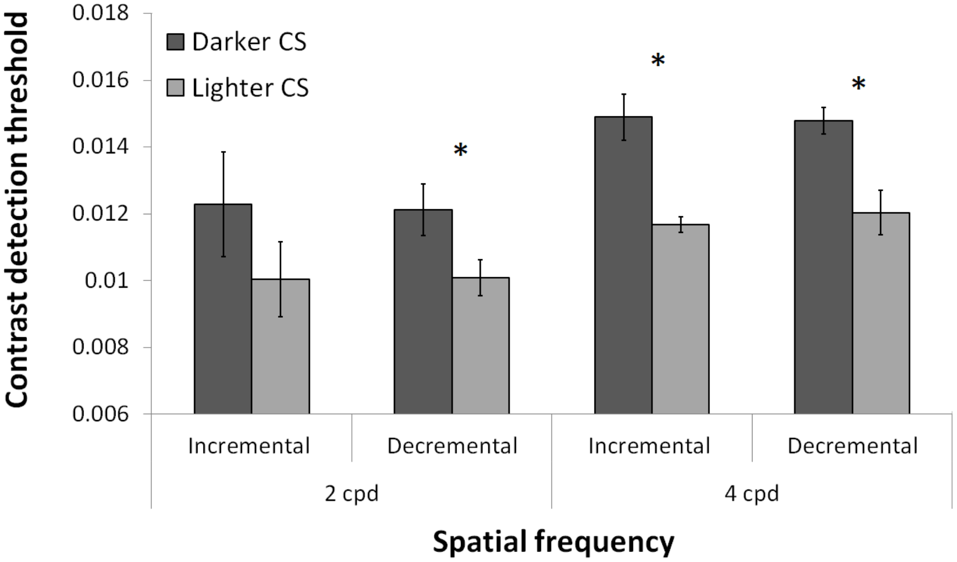

Figure 3.2: Results of contrast detection experiment using illusory checkerboard stimulus. Mean detection thresholds for the contrast gratings superimposed on darker or lighter context square across different contrast types and frequency levels are plotted. Detection threshold is lower for the gratings superimposed on equiluminant but perceptually lighter CSs. * $p < 0.05$. Error bars show ±1 SEM.

3.2 Results

Detection thresholds for incremental and decremental contrast patterns across two frequency levels are shown in Figure 3.2. Analyses showed that main effect of CS was statistically significant (F(1,4) = 132.45, $p < 0.001$). Mean detection threshold for the gratings superimposed on darker CS (M = 0.014, SEM = 0.001) was higher than that on the lighter CS (M = 0.011, SEM = 0.0004). However, main effect of contrast type (F(1,4) = 0.004, $p > 0.05$) and frequency (F(1,4) = 5.77, $p > 0.05$) was not statistically significant. Also, there was no significant interaction. Two-tailed paired-samples Student's t-test results showed that mean detection threshold for the gratings superimposed on darker CS was significantly higher than that on the lighter CS for all conditions tested (2 cpd decremental grating condition: t(4) = 5.18, $p < 0.05$; 4 cpd incremental grating condition: t(4) = 4.54, $p < 0.05$; 4 cpd decremental grating condition: t(4) = 3.58, $p < 0.05$;) except the 2 cpd incremental grating condition(t(4) = 2.64, $p = 0.057$). Because spatial frequency has not an effect on thresholds, we also averaged the

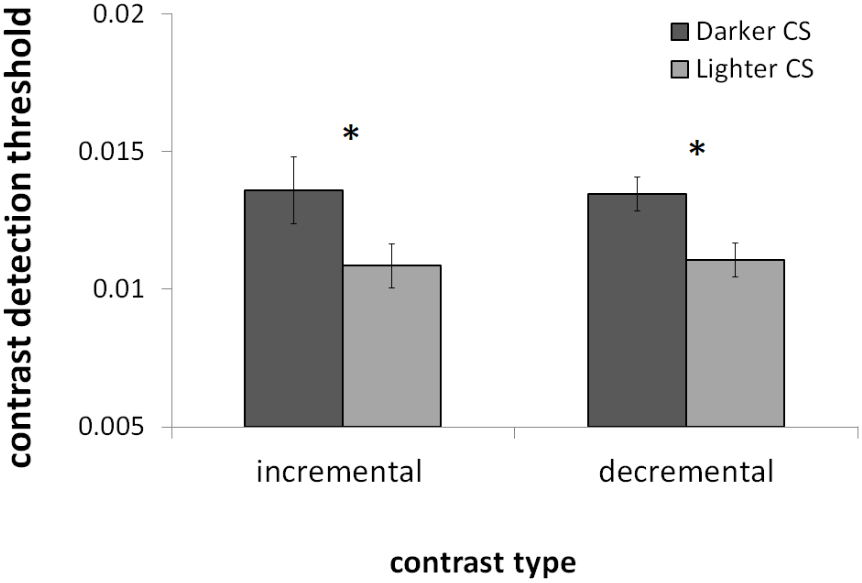

Figure 3.3: Results of contrast detection experiment using illusory checkerboard stimulus. Mean detection thresholds for the contrast gratings superimposed on darker or lighter context square across different contrast types are plotted. Because frequency did not have a main effect, thresholds were averaged over two frequency levels. Detection threshold is lower for both incremental and decremental gratings superimposed on equiluminant but perceptually lighter target regions. * $p < 0.01$. Error bars show ±1 SEM.

thresholds across frequencies (see Figure 3.3) and compared them from different CSs obtained under different contrast types using a two-tailed paired-samples Student's t-test. Also, mean proportion of correct responses averaged across participants and frequency levels and corresponding PFs are plotted in Figure 3.4 as a function of stimulus contrast. In the incremental grating condition, mean detection threshold for the gratings superimposed on darker CS (M = 0.0136, SEM = 0.0007) was higher than that on the lighter CS (M = 0.0108, SEM = 0.0006) and the difference was statistically significant (t(4) = 7.37, $p < 0.01$). The same effect was observed for decremental gratings. In the decremental grating condition, mean detection threshold for the gratings superimposed on darker CS (M = 0.0134, SEM = 0.0005) was higher than that on the lighter CS (M = 0.011, SEM = 0.0005) and the difference was statistically significant (t(4) = 4.66, $p < 0.01$).

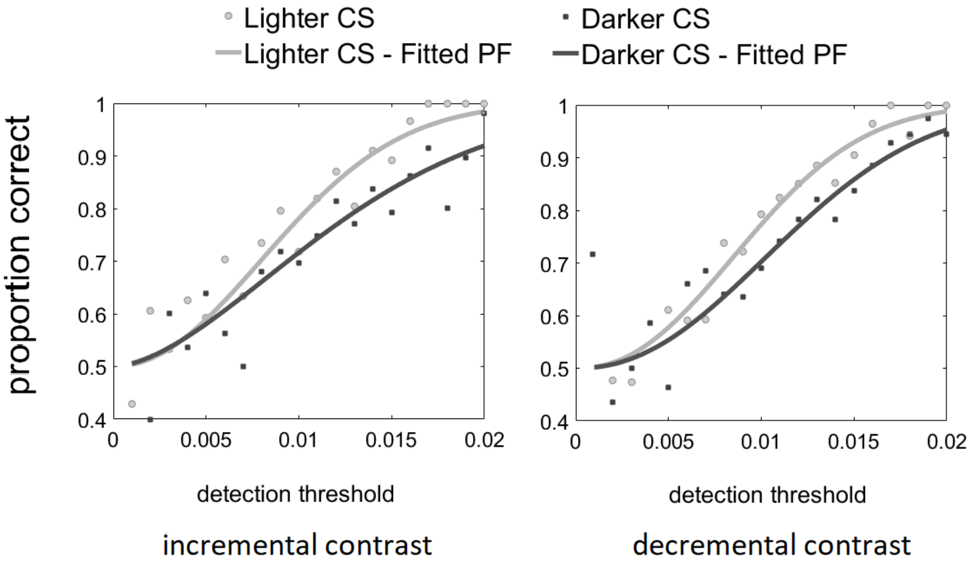

Figure 3.4: Mean proportion of correct responses averaged across participants and two frequency levels as a function of stimulus contrast, and corresponding psychometric functions (PF).

3.3 Summary and Discussion

Results showed that context-dependent lightness of the background affects contrast detection thresholds. In this experiment, gratings superimposed on equiluminant but perceptually lighter CSs were detected at relatively lower contrast levels than those superimposed on perceptually darker CSs. These results are partly consistent with our previous appearance results. For the incremental gratings, both threshold and perceived contrast are affected by the context-dependent lightness. However, for the decremental gratings, only threshold is affected by the context-dependent lightness, but not the perceived contrast.

It is well known that spatial frequency affects contrast perception in simple gratings [61, 14, 54, 55, 15, 56]. For all frequencies tested we found an effect of context-dependent background lightness on contrast detection threshold. However, frequency did not change the effect significantly although there was a trend ($p = 0.075$) seen in the Figure 3.2. Similarly, we could not find an effect of frequency on the appearance results either. We offered an explanation in the

Discussion Chapter (see Chapter 7) for the disagreement between our results and findings in the literature considering differences in experimental designs. Also, the limited number of frequency levels we could test in the threshold experiments might have led to the disagreement. We could not create gratings with higher frequencies in this experiment because of the limited dimensions of our monitor and the relatively small size of CSs on which we superimposed gratings. Therefore, we tested the effect of frequency on contrast detection thresholds again in the following experiment conducted using simultaneous brightness contrast stimulus.

Chapter 4

Contrast Detection Threshold Measurement Using Simultaneous Brightness Contrast Illusion

After showing the effect of context-dependent lightness on perceived contrast and contrast detection thresholds, we wanted to see whether the effect correlates with the strength of the illusory lightness effect. The checkerboard we used in our previous studies has a strong illusory effect. Therefore, we also wanted to test a subjectively weaker illusory lightness stimulus, namely the simultaneous brightness contrast stimulus (SBC, see an example in Figure 4.1). In this study, we measured perceived contrast and detection thresholds of gratings superimposed on the SBC stimulus. Besides, we tested higher frequency levels in this threshold experiment.

Figure 4.1: An example of simultaneous brightness contrast effect. Although the inner squares have equal luminance value, most observers have reported different brightness values [19].

4.1 Measurement of Perceived Contrast

4.1.1 Methods

4.1.1.1 Participants

Four participants (one male) including the author ZP participated in the experiments. The mean age was approximately 27.7 ranging from 25 to 32. All participants reported normal or corrected-to-normal vision, and had no history of neurological or visual disorders. Participants provided written informed consent and the experimental protocols were approved by the Human Ethics Committee of Bilkent University.

4.1.1.2 Stimuli and Design

The experimental software was prepared using the Java programming platform (http://hboyaci.bilkent.edu.tr/PsychWithJava/). The stimuli were presented on a CRT monitor (HP P1230, 22 inch, 1600 X 1200 resolution). Presentation of correct luminance values was ensured by using a gray scale look-up table prepared

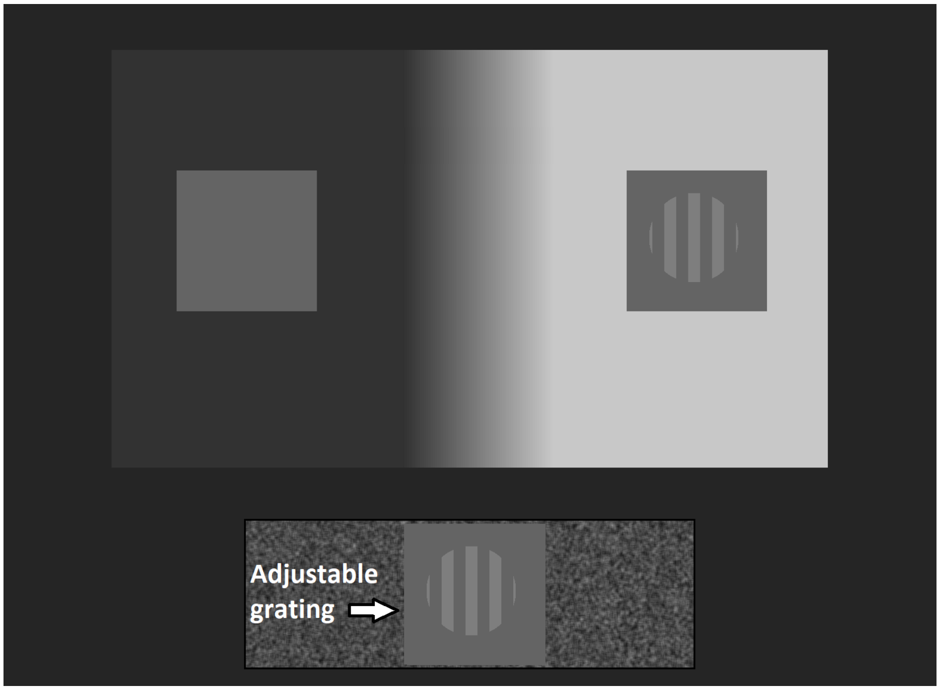

Figure 4.2: Task and procedure in the contrast adjustment experiment conducted using SBC stimulus. Participants were asked to adjust the contrast of a match grating to match that of the standard. Standard was always placed on one of the CSs. The match was placed on a square, which was placed on a random-noise background. The arrow, and the text "adjustable grating" were not shown on the screen during the experiment.

after direct measurements with a colorimeter (SpectroCAL, Cambridge Research Systems Ltd., UK). Participants were seated 75 cm from the monitor, and their heads were stabilized using a chin rest. Participants' responses were collected via a standard computer keyboard.

In this experiment, a typical SBC stimulus was used in order to create lightness illusion (see Figure 4.2). The stimulus was generated using the open source inkscape software (https://inkscape.org/en/). Although the small inner squares (context squares in SBC illusion, CSs) superimposed on left and right side of the image have identical luminance, our observers informally reported they look considerably different. In this stimulus, absolute value of contrast between background and inner squares kept identical (33% Michelson Contrast). The stimulus covered 15.2 by 11.4 degrees of visual angle. Approximate size of the inner squares was 3.2 by 3.2 degrees of visual angle. Luminance of the context square was 17.4 cd/m^2 (mean image luminance was 18.7 cd/m^2). Participants' task was to perceptually adjust the contrast of a match grating to match that of the standard grating. The standard was always placed on one of the CSs. The match grating was placed on a square that had the same luminance and the same size as the CS, which in turn was placed on an external random-noise background (Figure 4.2). Contrast of the gratings was defined by Weber Contrast. Incremental gratings with either 0.1, 0.3, or 0.6 contrast levels and frequency of 2 cpd were tested in a single session. Adjustment was done in $\Delta C = 0.1$ steps by the use of left and right arrow keys and fine tuned adjustment was done in $\Delta C = 0.01$ steps using the up and down arrow keys. In each trial the contrast of the standard was pseudo-randomly chosen among the contrast levels tested and balanced across the session. Initial contrast of match was determined randomly at the start of each trial. Each session contained 30 trials with 5 repetitions for every combination of conditions (3 contrast levels × 2 CS positions × 5 repetitions).

4.1.1.3 Data Analysis

The analyses were performed on an effect scores defined previously in Equation 2.1. In order to test whether the effect score is different than "0" we conducted one-sample two-tailed Student's t-test in SPSS. Further analyses were conducted using one-way ANOVA in SPSS in order to assess the effect of different contrast levels.

4.1.2 Results

Raw settings are shown in Figure 4.3. Analyses showed that there was no difference in effect scores across different contrast levels (F(2,6) = 1.27, $p > 0.05$). However, mean effect score was positive ($\overline{\rho}_C = 0.049$, SEM = 0.01) and significantly different than zero (t(3) = 3.67, $p < 0.05$). Further analyses revealed that only effect score significantly different than zero was at 0.6 contrast level ($\overline{\rho}_C$

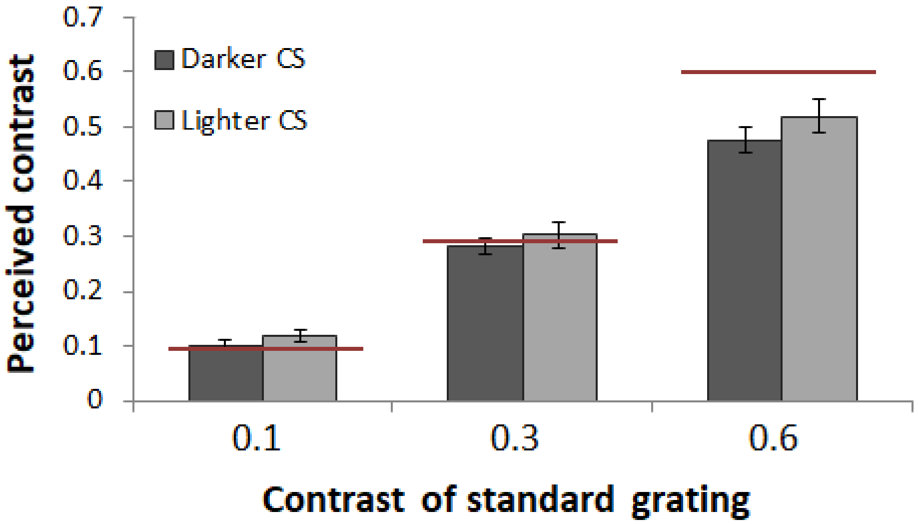

Figure 4.3: Mean settings in the contrast adjustment experiment conducted using SBC stimulus. Red horizontal lines shows the actual contrast under that condition. Error bars show ±1 SEM.

= 0.04 SEM = 0.0073; t(3) = 5.38, $p < 0.05$). At 0.1 contrast level ($\overline{\rho}_C = 0.07$ SEM = 0.03; t(3) = 2.39, $p > 0.05$) and 0.3 contrast level ($\overline{\rho}_C = 0.03$ SEM = 0.01; t(3) = 1.82, $p > 0.05$) the effect score was not different than zero. In other words, perceived contrast was higher only when the grating with 0.6 contrast was superimposed on the perceptually lighter CS.

4.1.3 Intermediate Summary and Discussion

Results of this experiment show that context-dependent lightness affects perceived contrast of an incremental grating even when we manipulated lightness using a weaker illusory stimulus, simultaneous brightness contrast. The same grating appears to have higher contrast when it is superimposed on an equiluminant but perceptually lighter CS of SBC illusion. However, as we predicted the effect was also weaker compared to experiments conducted using illusory cylinder stimulus (for cylinder stimulus mean effect score: $\overline{\rho}_C = 0.14$; SEM = 0.02; t(5) = 8.03, $p < 0.01$; for SBC stimulus mean effect score: $\overline{\rho}_C = 0.049$ SEM = 0.01; (t(3) = 3.67, $p < 0.05$).

4.2 Measurement of Contrast Detection Threshold

4.2.1 Methods

4.2.1.1 Participants

Four female participants including the author ZP participated in the experiments. The mean age was approximately 25.5 ranging from 23 to 28. All participants reported normal or corrected-to-normal vision, and had no history of neurological or visual disorders. Participants provided written informed consent and the experimental protocols were approved by the Human Ethics Committee of Bilkent University.

4.2.1.2 Stimuli and Design

The experimental software was prepared using the Java programming platform (http://hboyaci.bilkent.edu.tr/PsychWithJava/). The stimuli were presented on a CRT monitor (HP P1230, 22 inch, 1024 X 768 resolution). To be able to present very fine-grained contrast differences, the dynamic luminance range of the monitor is increased (14-bit luminance resolution) using a digital-to-analog converter (Bits#, Cambridge Research Systems Ltd., UK). Presentation of correct luminance values was ensured by using a 14-bit gamma-corrected gray scale lookup table prepared after direct measurements with a colorimeter (SpectroCAL, Cambridge Research Systems Ltd., UK). Participants were seated 120 cm from the monitor, and their heads were stabilized using a chin rest. Participants' responses were collected via a standard computer keyboard.

The experimental protocol is shown in Figure 4.4. In the experiment, an adaptive two-interval forced-choice procedure (2-IFC) was used. At the beginning of each trial, either original SBC stimulus or the mirror-symmetric version of it is

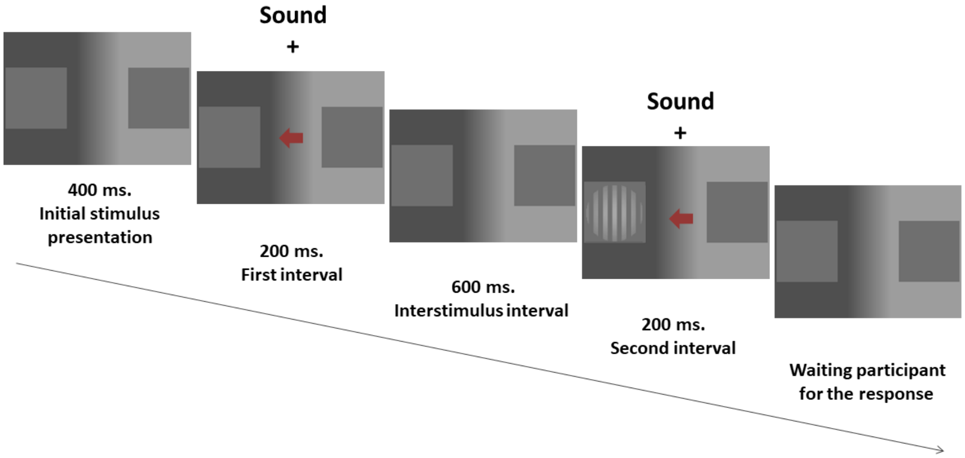

Figure 4.4: Protocol for the detection threshold experiment conducted using simultaneous brightness contrast. At the beginning of each trial, either original or the mirror-symmetric version of the simultaneous brightness contrast stimulus was presented randomly. An arrow was used to inform participants about the side of the stimulus on which the grating would be presented. Gratings were superimposed on only one of the CSs, either darker or lighter, throughout a session. In each trial, grating is presented at one of the intervals selected randomly. Participants are asked to decide in which interval the grating is presented. Participants are allowed to look at target CS directly.

presented randomly. Gratings weighted by two-dimensional isotropic Gaussian envelopes were superimposed on only one of the CSs, throughout a session. Luminance of the context square was 17.4 cd/m^2 (mean image luminance was 18.7 cd/m^2). The stimulus covered almost the entire computer screen (approximately 18 by 12.5 degrees of visual angle). Approximate size of the inner squares was 6.2 by 6.2 degrees of visual angle. An arrow was used to inform participants about the side where the grating would be presented. Each trial started with a 400-millisecond (ms) illusory stimulus presentation, followed by two intervals each presented for 200 ms. Intervals were separated by a 600-ms ISI, the illusory stimulus remained on the screen during the ISI (Figure 4.4). A beep-sound was presented at the beginning of each interval in order to inform participants that the interval begins. The grating was randomly presented at one of the intervals. Participants were asked to decide the interval in which the grating was presented. Two interleaved staircases with a starting point 0.002 and 0.02 contrast level (80 trials each, 160 trials in total) were applied in a single session. After each trial, contrast of the next grating was decided based on the previous responses following a 1-up 3-down adaptive staircase with 0.001 contrast steps. The contrast of the grating was decreased one step following three consecutive correct answers, and increased one step following an incorrect answer. There was no time constraint; the illusory SBC stimulus remained on the screen until the participant made a response. Observers participated in 12 experimental sessions (2 CSs (perceived darker or lighter) X 2 contrast type (incremental or decremental) X 3 frequency levels (1, 7 or 14 cpd)).

4.2.1.3 Data analysis

Data were first analyzed with Palamedes toolbox [60] to find the detection threshold (79% success) in Matlab (R2016b, MathWorks). A PF was fit to the raw data with a Weibull function and lapse rate was fixed to 0. Standard error of the thresholds were calculated for each participant using bootstrapping. Mean thresholds averaged across observers and standard error of mean for each condition were computed and plotted in figures. For decremental contrasts, before computing

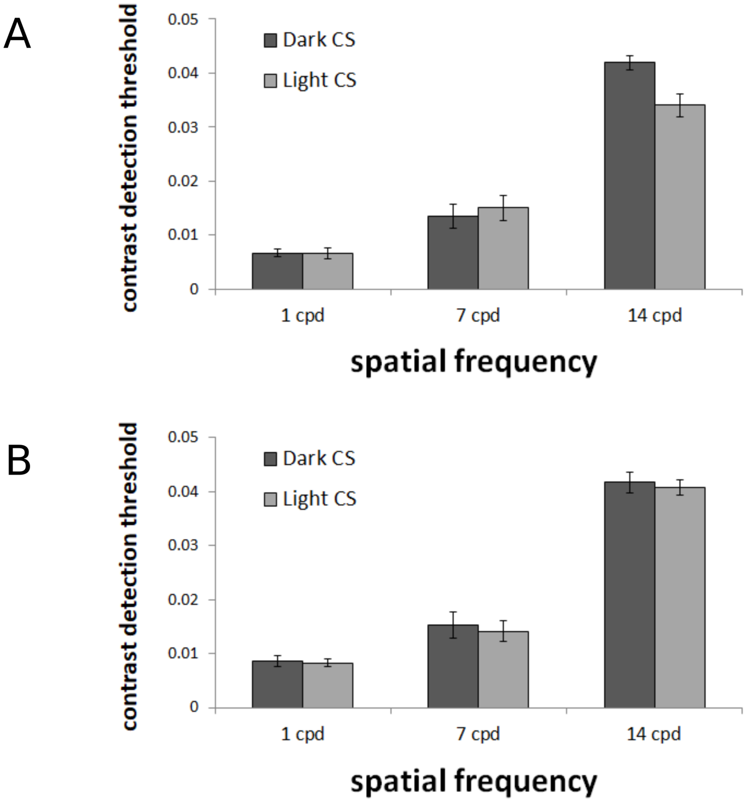

Figure 4.5: Results of contrast detection experiment using simultaneous brightness contrast stimulus. Mean detection thresholds for the contrast gratings superimposed on darker or lighter context square across different frequency levels are plotted. (A) Incremental grating condition. (B) Decremental grating condition. Differently from the experiments conducted using illusory checkerboard stimulus, mean detection threshold for the gratings superimposed on darker was not significantly higher than that on the lighter CS. Error bars show ±1 SEM.

the threshold, we first converted the levels to positive values. We applied repeated measures ANOVA with three factors (contrast type, CS, frequency) and Bonferroni corrected pairwise comparisons on the estimated threshold values in SPSS.

4.2.2 Results

Results are shown in Figure 4.5. Also, mean proportion of correct responses averaged across participants as a function of stimulus contrast and corresponding PFs are plotted in Figure 4.6. Here, mean proportion of correct responses of 1 cpd spatial frequency condition was shown as a representative of all frequency levels tested. Analyses showed that differently from the experiments conducted using illusory checkerboard stimulus, main effect of CS was not statistically significant (F(1,3) = 5.36, $p > 0.05$). Mean detection threshold for the gratings superimposed on darker CS (M = 0.021, SEM = 0.001) was not significantly higher than that on the lighter CS (M = 0.02, SEM = 0.001). Also, main effect of contrast type (F(1,3) = 4.57, $p > 0.05$) was not statistically significant. However, main effect of frequency was significant (F(1,3) = 274.39, $p < 0.001$). Also, there was no significant interaction. Bonferroni corrected pairwise comparisons showed that the detection thresholds at 1 and 14 cpd (M = 0.008, SEM = 0.001 for 1 cpd; M = 0.04, SEM = 0.0001 for 14 cpd; $p < 0.001$) and 7 and 14 cpd (M = 0.014, SEM = 0.002 for 7 cpd; $p < 0.01$) was significantly different.

4.2.3 Intermediate Summary and Discussion

In this experiments we could not find an effect of lightness on contrast detection thresholds, although there is a trend in some conditions similar to findings of experiments with the checkerboard stimulus. Since the context-dependent lightness effect in adjustment experiment was considerably weaker when we used SBC illusion, this result is not very surprising. Also, spatial frequency affected threshold performance in this experiment. Detection thresholds increased as the spatial frequency increased.

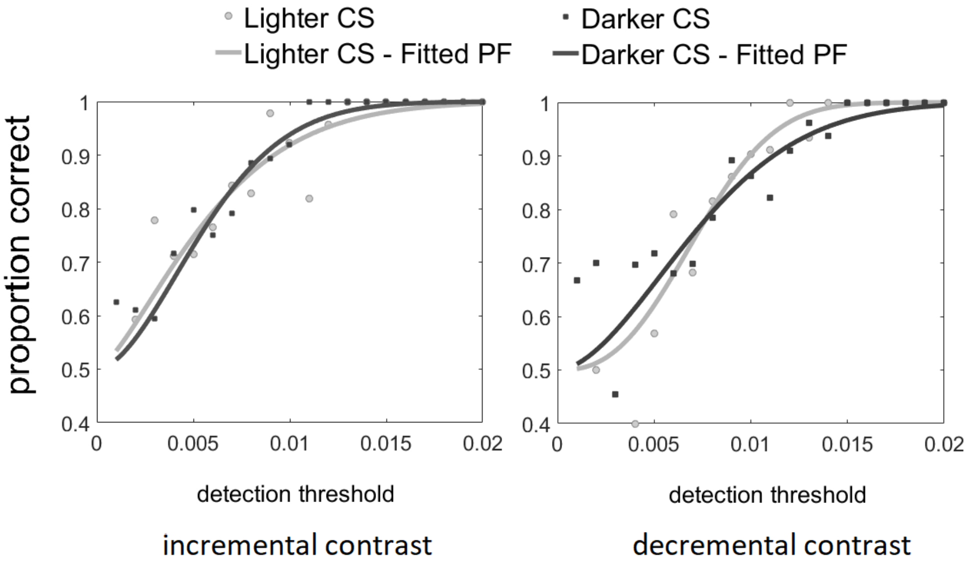

Figure 4.6: Mean proportion of correct responses averaged across participants for 1 cpd spatial frequency condition as a function of stimulus contrast, and corresponding psychometric functions (PF).

4.3 Summary and Discussion

Results of adjustment and threshold experiments conducted using SBC illusion support our prediction that the context-dependent lightness effect correlates with the strength of the illusory lightness. When the lightness illusion is weaker, the context-dependent lightness effect is much smaller or absent. Also, differently from the previous experiments done with the illusory checkerboard stimulus, here we found an effect of frequency. In this experiment, we used bigger gratings in a relatively simpler contextual environment. Previously, it has been shown that spatial frequency filters' resolution decreases as the retinal eccentricity increases [62]. Therefore, bigger gratings could be processed by the filters whose resolution is relatively weaker and this may affect the behavioral performance negatively. This could potentially explain the discrepancy between the previous and the present results.

Chapter 5

fMRI of Perceived Contrast in Context

In our previous experiments, we showed that behavioral performance both on appearance and detection threshold measures is affected by the context-dependent lightness of the background on which contrast patterns are superimposed. In order to investigate the underlying neuronal mechanisms of this effect, we conducted an fMRI study. Also, we replicated appearance experiments in the scanner to ensure that the stimulus conditions were identical for behavioral and fMRI experiments.

5.1 Behavioral Appearance Experiment in the Scanner

5.1.1 Methods

5.1.1.1 Participants

Eight participants (four female) including the author ZP participated in the experiments. The mean age was approximately 25.6 ranging from 21 to 29. All participants reported normal or corrected-to-normal vision, and had no history of neurological or visual disorders. Participants provided written informed consent and the experimental protocols were approved by the Human Ethics Committee of Bilkent University.

5.1.1.2 Stimuli and Design

For this experiment, we replicated our previous adjustment experiment while participants were lying in the scanner. Visual stimuli were presented on a MR-compatible LCD monitor (TELEMED, 32 inch, 1920 X 1080 resolution) that was viewed by participants through a mirror located above their eyes inside the scanner. The viewing distance was 135 cm. The monitor was calibrated using a SpectroCAL (Cambridge Research Systems Ltd.) colorimeter.

Differently from previous experiments, we only tested one contrast and one frequency level that we used in the fMRI experiment (0.2 incremental or decremental contrast, 2 cpd spatial frequency). Participants' task was to perceptually adjust the contrast of a match grating to match that of the standard grating. The standard was always placed on one of the CSs. The match grating was placed on a square that had the same luminance and approximately the same dimensions as the CS, which in turn was placed on an external random-noise background. Contrast of the rectified square-wave gratings were defined by Weber Contrast.

Adjustment was done in 0.02 steps using buttons of a MRI-compatible response pad. We used the version of the checkerboard stimulus in which CS luminance was 2.86 cd/m^2. Stimuli were presented on a black background. In each trial the contrast of the match had the same contrast polarity as the standard and its initial contrast was determined randomly at the start of each trial. Each session contained 10 trials with 5 repetitions for every combination of conditions (1 contrast level X 2 CS positions X 5 repetitions). Incremental and decremental contrast patterns were tested in different blocks.

5.1.1.3 Data Analysis

Analyses were performed on averaged perceived contrast scores. First, a repeated-measures ANOVA was conducted in order to test two factors: contrast type (two levels: incremental, decremental), and CS (two levels: darker, lighter). Also, we conducted two-tailed paired-samples Student's t-test in SPSS in order to test whether perceived contrasts of gratings superimposed on either darker or lighter CSs are significantly different.

5.1.2 Results

Results are shown in Figure 5.1. The ANOVA results showed that main effect of contrast type (F(1,7) = 0.026, $p > 0.05$) and main effect of CS (F(1,7) = 4.15, $p > 0.05$) was not statistically significant. However, the interaction between contrast type and CS (F(1,7) = 31.45, $p < 0.01$) was significant. For the incremental grating condition, perceived contrast of gratings superimposed on lighter CSs was higher than those superimposed on darker CS (t(7)= 4.26, $p < 0.01$). For the decremental grating condition, the difference was not significant (t(7)= -1.05, $p > 0.05$). In this experiment, consistent with our previous adjustment experiments, we found that perceived contrast increased with context-dependent lightness of the background for incremental gratings, but not for decremental gratings.

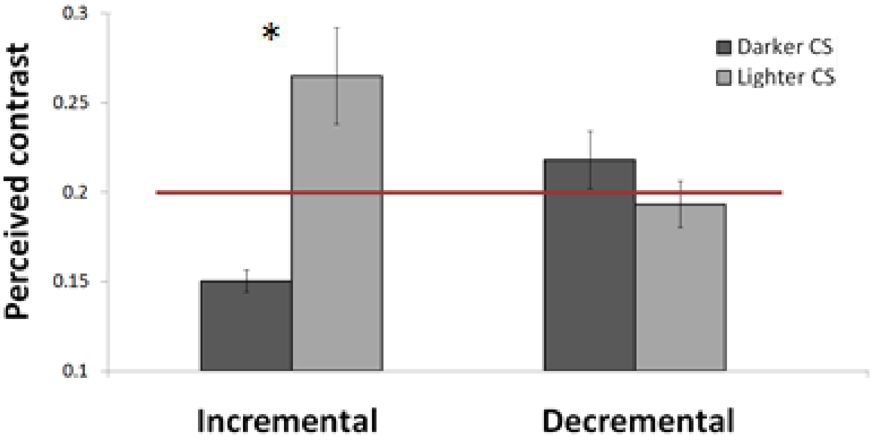

Figure 5.1: Mean settings in the perceived contrast experiment in the scanner. Red horizontal line corresponds to the actual contrast. Consistent with previous adjustment experiments, perceived contrast increased with context-dependent lightness of the background for incremental gratings, but not for decremental gratings. * $p < 0.01$. Error bars show ±1 SEM.

5.2 fMRI Experiment

5.2.1 Methods

5.2.1.1 Participants

Eight participants (four female) including the author ZP participated in the experiments. The mean age was approximately 25.6 ranging from 21 to 29. All participants reported normal or corrected-to-normal vision, and had no history of neurological or visual disorders. Participants provided written informed consent and the experimental protocols were approved by the Human Ethics Committee of Bilkent University. All participants have participated in the behavioral appearance experiments in the scanner (Section 5.1).

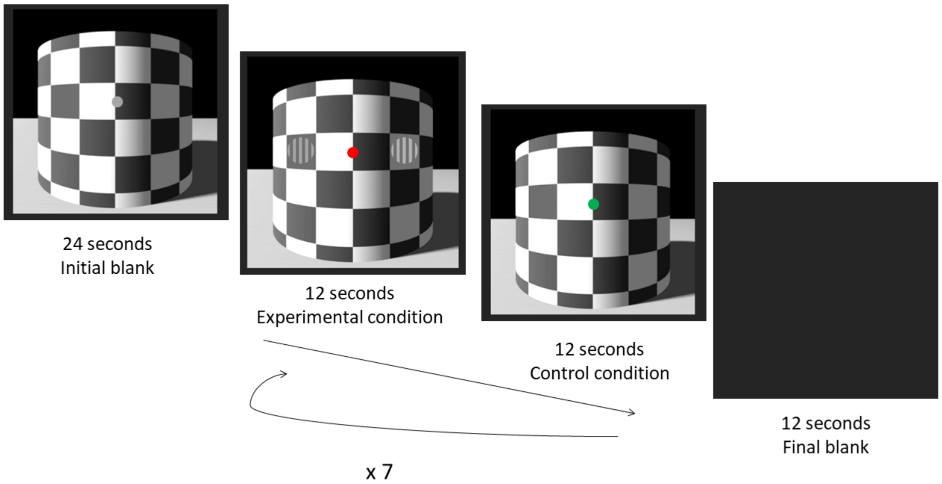

Figure 5.2: Protocol for the fMRI study. In each experimental block, gratings are flickering on the CSs. During the block, one of the gratings is frozen for 500 milliseconds randomly in each 2-4 seconds.

5.2.1.2 Stimuli and Design

Monitor properties were the same with the behavioral experiment in the scanner. The fMRI experiment included an anatomical scan, a functional localization scan, and eight experimental scans. The illusory checkerboard stimulus was used in the experiments. Photometrically identical gratings were superimposed on both CSs simultaneously. Gratings were flickering at 4 Hz to avoid adaptation of neurons. In the first 24 seconds only illusory checkerboard stimulus was presented on the screen without gratings on CSs, and in the last 12 seconds, they viewed a uniform dark gray background. A block design experiment consisting of two conditions was conducted. First condition was experimental block and the second condition was control block. In the experimental block, participants viewed flickering gratings on CSs. In the control block, only the illusory checkerboard stimulus was presented. Each experimental block was followed by the control block, and this circle was repeated seven times. Each block lasted 12 seconds and participants viewed the fixation mark throughout the experiment (see Figure 5.2).

In literature it has been shown that spatial attention alters both visual perception [63, 62, 64] and neural activities in visual pathways [65]. Therefore, spatial attention was controlled in this study. We examined how manipulating attention modulates the effect of lightness on contrast perception in two conditions. Participants were required to fixate either on fixation mark or on the gratings. We increased the attentional load at fixation in order to control top-down attentional mechanisms and evaluate the bottom-up (sensory-driven) responses of early visual areas [66, 67]. In the two attentional condition, the presentation paradigm was identical only the tasks differed. In the attend-to-fixation condition, participants were required to detect and report the changes in color of the fixation mark by pressing the response buttons. In the attend-to-stimulus condition, one of the flickering gratings froze for 500 milliseconds randomly in every 2000-4000 milliseconds. Participants were asked to fixate the dynamic fixation mark, and they are required to detect the grating that has been frozen. Eight fMRI scans were applied; two for different attention levels and two for different contrast types. Each condition was repeated two times in one of which mirror-symmetric version of the stimulus was presented. Also, functional regions of interest (ROIs) were identified in a different scan within the main experimental session.

5.2.1.3 Anatomical and Functional Region of Interest (ROI) localization

We conducted a separate fMRI session in order to identify retinotopic visual areas. We used the standard phase-encoded retinotopic mapping methods (see an example in Figure 5.3) based on neural responses to rotating wedge and expanding or contracting rings of flickering black and white checks [68, 69].

We identified functional ROIs in a different scan within the experimental session. We functionally localized the cortical areas corresponding to the spatial location of gratings on CSs using conventional methods in which participants viewed flickering gratings on a trapezoid-shaped background whose luminance, size and locations were exactly the same as the CSs (see Figure 5.4). Also, physical properties of the gratings were identical with the ones used in actual

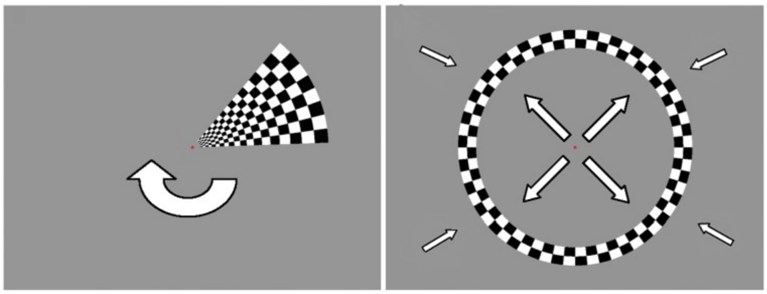

Figure 5.3: An example of flickering black and white checks stimuli used in conventional retinotopy experiments. (LEFT) Rotating wedge. (RIGHT) Expanding or contracting rings.

fMRI experiment. In the first 24 seconds subjects viewed only the trapezoid-shaped background without gratings. In the experimental block, participants viewed flickering gratings on the trapezoid-shaped background. In the control block, there were no gratings on this background. Each experimental block was followed by the control block, and this circle was repeated seven times. Each block lasted 12 seconds and participants viewed the fixation mark and they were required to detect changes in its color throughout the experiment.

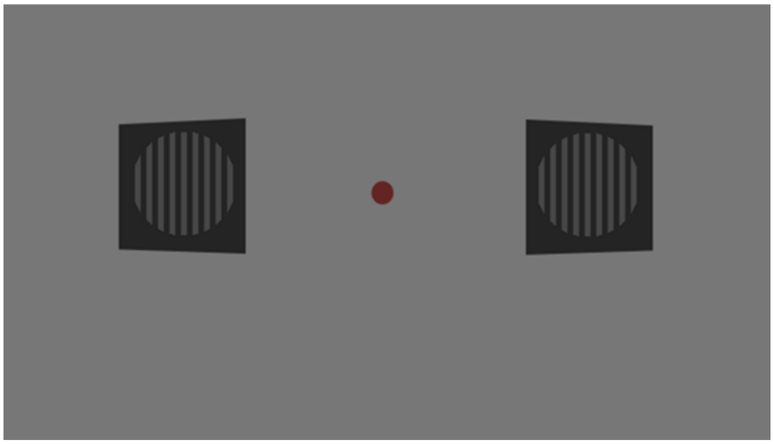

Figure 5.4: Functional ROI stimulus. Flickering gratings were shown on a trapezoid-shaped background whose luminance, size and locations were exactly the same as the context squares. Participants viewed the fixation mark and they were required to do fixation task by detecting the changes in its color. The only difference with the experimental stimulus was absence of the illusory checkerboard stimulus.

5.2.1.4 MRI data acquisition

Experiment was conducted at the National Magnetic Resonance Research Center (UMRAM), Bilkent University. Scanning was performed on a 3 Tesla scanner (Siemens Trio) using a thirty two-channel phase-array head coil. Each session began with an anatomical scan using a high resolution T1-weighted 3D MPRAGE sequence (1x1x1 mm^3 resolution, TE: 3.02 ms, TR: 2600 ms, FOV read: 256, FOV phase: 87.5, flip angle: 8 degrees, slice thickness: 1 mm). Functional data were acquired with an echo-planar imaging (EPI) sequence (TR: 2000 ms, TE: 35 ms, flip angle: 75 degrees, slice thickness: 3 mm, number of slices: 30, FOV: 192x192 mm^2, matrix: 64x64, slice orientation: parallel to calcarine sulcus).

5.2.1.5 fMRI data processing and analyses

MRI data were processed using BrainVoyager QX (Brain Innovation, Maastricht, The Netherlands). First white matter-gray matter boundaries are drawn, then the cortex is constructed and inflated. Functional images were preprocessed to correct for 3-dimensional head motion, to filter out low temporal variations (below 0.015 Hz) and to remove linear trend. The functional images were first transformed into AC-PC space and then aligned with the anatomical image.

Boundaries between visual areas were drawn based on the Linear Correlation Maps of retinotopic mapping section. Functional ROIs within each visual area were identified by a General Linear Model procedure on the inflated cortices. The time course and event-related average of fMRI signals of each functional scan were extracted from pre-defined ROIs. In order to extract the time course of BOLD responses, the data across all the voxels within the ROI was averaged and per cent BOLD signal change, normalized by the mean BOLD signal across the scan, was computed for each time point. Next trial-onset-locked event-related averaging was performed, and the average response between 8 and 12s of control condition (0-4 secs. before the stimulus onset) was subtracted from the average response from forth to seventh volume (between 6 and 14s after the stimulus onset) of the experimental block as the average response for further analyses. Repeated-measures ANOVA was conducted in order to test three factors: contrast type (two levels: incremental, decremental), attentional condition (two levels: attend-to-stimulus, attend-to-fixation), and CS (two levels: darker, lighter). Additionally, for each condition, data from darker and lighter CS was compared by conducting a two-tailed paired-samples Student's t-test in SPSS.

5.2.2 Results

BOLD response time courses within V1 for incremental and decremental contrast stimuli in two attention conditions are shown in Figure 5.5, and event-related averages in different visual areas within pre-defined functional ROIs are plotted in Figure 5.6. Also, accuracy of participants on behavioral attention tasks they performed during fMRI scanning is plotted in Figure 5.7 in order to show that they performed very well on both attention tasks. Below, detailed results are reported separately for each visual area.

5.2.2.1 Activity within pre-defined functional ROI in V1

Results are shown in Figure 5.6. Analyses showed that main effect of CS (F(1,7) = 21.56, $p < 0.01$) and main effect of attentional condition (F(1,7) = 8.84, $p < 0.05$) were statistically significant. However, main effect of contrast type was not significant (F(1,7) = 0.035, $p > 0.05$). Also, there was no significant interaction. Two-tailed paired-samples Student's t-test results showed that for the incremental grating condition, the BOLD activity was increased when the grating was superimposed on perceptually lighter CS both for the attend-to-stimulus (t(7)= 3.29, p = 0.013; not significant after Bonferroni correction) and the attend-to-fixation (t(7)= 6.64, $p < 0.001$) conditions. The same pattern was observed for the decremental grating condition that the BOLD activity was increased when the grating was superimposed on lighter CS both for attend-to-stimulus (t(7)= 4.007, $p < 0.01$) and attend-to-fixation (t(7)= 4.21, $p < 0.01$) conditions. Results

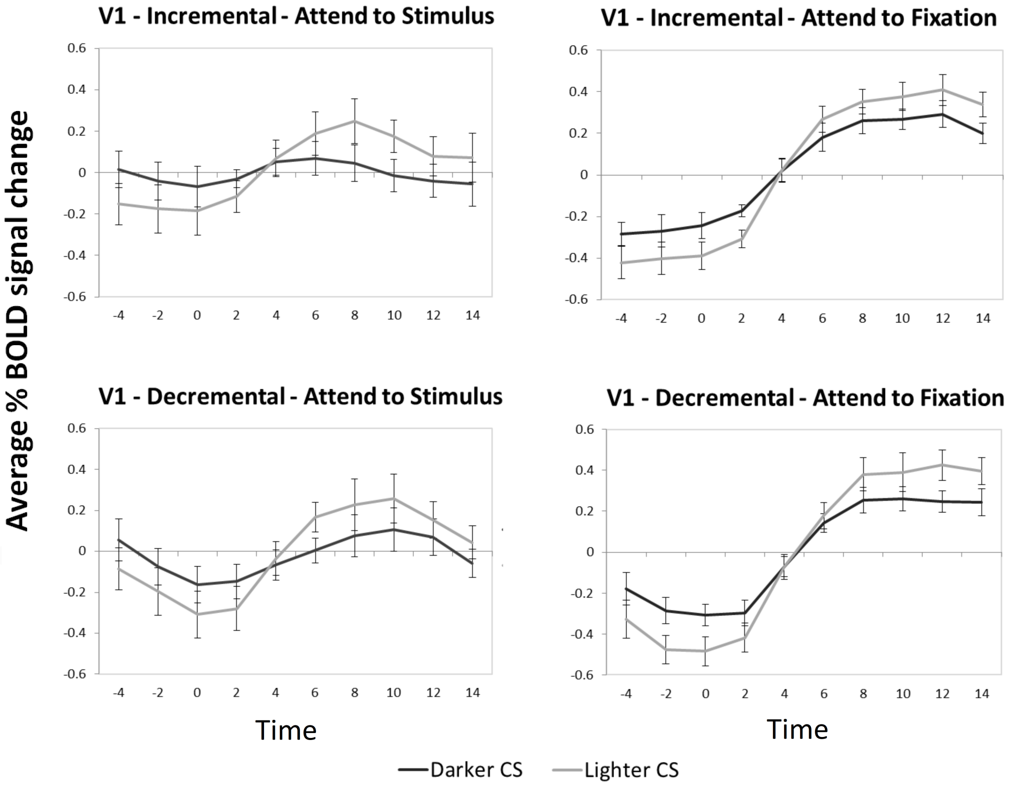

Figure 5.5: BOLD response time courses in seconds for incremental and decremental contrast stimuli from V1 among two different attention conditions. "0" point corresponds to onset of experimental condition. In each condition, the BOLD activity corresponding to lighter CS is larger. Error bars show ±1 SEM.

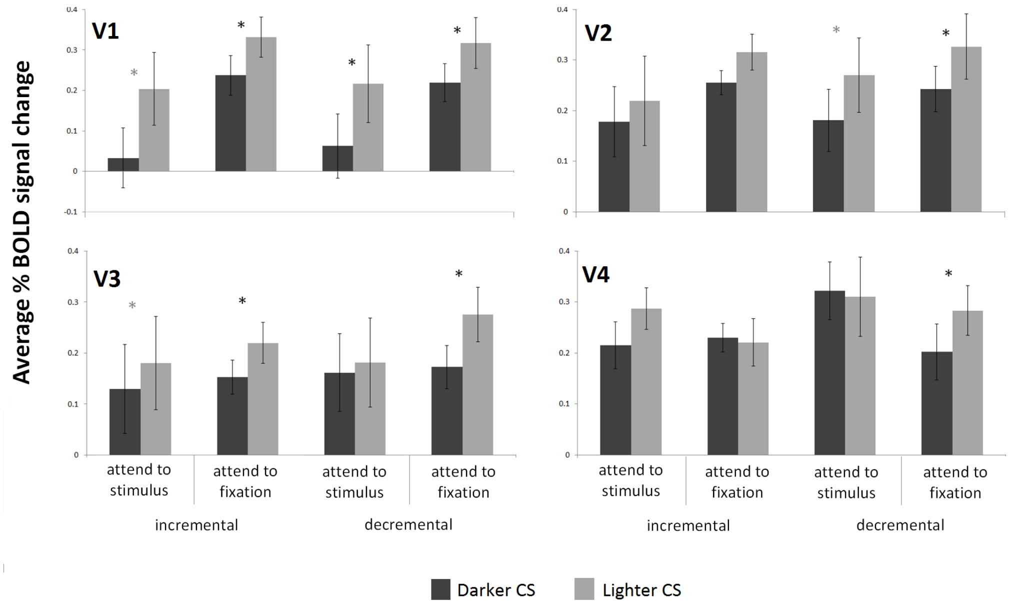

Figure 5.6: Results of fMRI experiments. For each condition, trial-onset-locked event-related averages in different visual areas within pre-defined functional ROIs were calculated for each of eight subjects. The average response between 8 and 12s before the stimulus onset was subtracted from the average response from third to sixth volume (between 6 and 14s after the stimulus onset) of the experimental block and plotted here as the averaged %BOLD signal change. * $p < 0.05$ (Lighter *: not significant after Bonferroni correction). Error bars show ±1 SEM.

clearly showed that for both contrast types, BOLD activity in V1 increased significantly when identical gratings were superimposed on perceptually lighter CS for both attention conditions.

5.2.2.2 Activity within pre-defined functional ROI in V2

Results are shown in Figure 5.6. ANOVA results revealed that the only significant main effect was seen for the CS (F(1,7) = 10.44, $p < 0.05$). Also, there was no significant interaction. Two-tailed paired-samples Student's t-test results showed that for the incremental grating condition, the BOLD activity did not change depending on the gratings on CSs (attend-to-stimulus condition: t(7)= 1.18, p = 0.27; attend-to-fixation condition: t(7)= 1.99, p = 0.08). However, for the decremental grating condition, the BOLD activity was increased when the

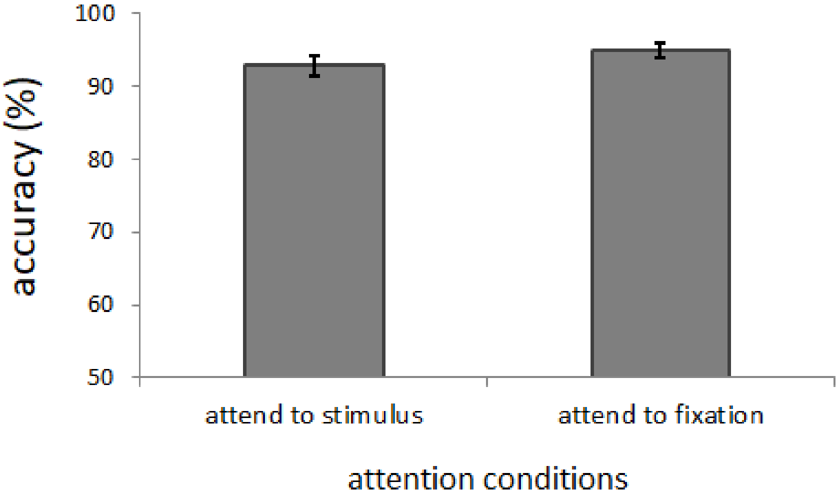

Figure 5.7: Mean accuracy of participants on attention tasks they performed during fMRI scanning. Participants performed well in both attention tasks. Error bars show ±1 SEM.

grating was superimposed on lighter CS both for attend-to-stimulus (t(7)= 3.22, p = 0.015; not significant after Bonferroni correction) and attend-to-fixation (t(7) = 4.58, p =0.003) conditions.

5.2.2.3 Activity within pre-defined functional ROI in V3

Results are shown in Figure 5.6. Similar with the activation in V2, ANOVA analyses showed that the only significant main effect was observed for the CS (F(1,7) = 16.64, $p < 0.01$). Also, there was no significant interaction. Additional t-test analyses revealed that the BOLD activity was increased when the grating was superimposed on perceptually lighter CS for incremental grating condition both for attend-to-stimulus (t(7)=2.64, p = 0.033; not significant after Bonferroni correction) and attend-to-fixation (t(7)=3.85, $p < 0.01$) conditions. For decremental gratings condition BOLD increase in attend-to-stimulus condition was not significant (t(7)=1.46, $p > 0.01$), but the difference was significant for attend-to-fixation condition (t(7)=4.06, $p < 0.01$).

5.2.2.4 Activity within pre-defined functional ROI in V4

We could not define ROI in V4 for one participant. Therefore, analyses were conducted using data from seven participants. Results are shown in Figure 5.6. ANOVA and two-tailed paired-samples Student's t-test results showed that there was no significant activity change in V4 except that the difference was significant for the decremental grating attend-to-fixation condition (t(6)=4.88, $p < 0.01$).

5.3 Summary and Discussion

In our previous experiments, we showed that the perceived contrast of rectified square-wave gratings is affected by the context-dependent lightness. Except decremental contrast patterns, when identical gratings are superimposed on equiluminant backgrounds, the one on perceptually lighter background appeared to have higher contrast. In order to investigate the underlying neuronal mechanisms of this effect, we conducted an fMRI study. In a block design, we superimposed identical flickering gratings simultaneously on perceptually darker and lighter CSs. We tested both incremental and decremental contrast patterns in two attention conditions called "attend-to-stimulus" and "attend-to-fixation". Our fMRI results showed that although the physical properties of the local stimuli that fall within our pre-defined ROIs are identical, there was a difference in BOLD signal especially in primary visual cortex (V1) correlating with the perceptual effect. More specifically, when identical gratings are superimposed on equiluminant backgrounds, the one on the perceived-lighter background elicited higher BOLD activity at all conditions we tested (incremental vs. decremental; attend-to-stimulus vs. attend-to-fixation).

Our results highlighted an interesting relationship between behavioral and neural data. Namely, fMRI results are not completely in line with the behavioral appearance results (see Section 2.3 and 5.1). For incremental gratings, perceived contrast increased with the increase in context-dependent lightness of the background. fMRI results were in agreement with this pattern. However, for decremental gratings, although there was no behavioral effect in the appearance experiment, increased BOLD signal change was observed for the condition that decremental gratings were superimposed on the lighter CS. Interestingly, pattern of neural activity only matched with the pattern of behavioral findings at threshold level (see Chapter 3). At threshold level, context-dependent lightness effect was seen both for incremental and decremental contrast patterns and there was no difference between these contrast types. Similarly in fMRI experiments, the effect was found for both contrast types and there was no difference between them. Since our BOLD results correlates better with threshold measures than the appearance measures, we thought that the BOLD activity we observed in V1 might better correspond to detection, but not the identification mechanism. Therefore, our results might be a neural evidence of the distinct mechanisms underlying detection and identification that Hillis and Brainard [9] showed behaviorally. In order to investigate this relationship further and systematically, we conducted additional behavioral threshold and fMRI experiments explained in the next chapter (see Chapter 6).

Chapter 6

Linking Behavioral and Neural Data

Our previous fMRI results are not completely in line with the behavioral appearance results. Instead, they are similar to the those of threshold measures. Considering this pattern in the results, the BOLD activity in V1 may better correspond to detection, but not the identification mechanism. Thus, the BOLD activity we observed in V1 might be a neural evidence of the distinct mechanisms that mediates object detection and identification shown behaviorally before [9].

According to Hillis and Brainard [9], detection mechanism can be modeled by both detection and discrimination threshold measures. Therefore, if fMRI activity we observed corresponds to detection mechanism, it should also correlate well with contrast discrimination thresholds. Previously, it has been shown that BOLD activity in early visual areas is consistent with the behavioral contrast discrimination thresholds [70]. Therefore, if BOLD activity corresponds to detection mechanism, then we expect to predict discrimination thresholds from corresponding BOLD activities. Therefore, in this study, we conducted additional behavioral and fMRI experiments in order to compare the behavioral and neural results systematically. In the behavioral experiments, we tested the context-dependent lightness effect both on detection and discrimination thresholds. Later, we conducted an fMRI study in order to examine the relationship between behavioral and neural data in detail. Also, an alternative experiment was conducted in order to investigate the relationship between behavioral and neural data. Details of this experiment can be seen in Appendix B.

6.1 Contrast Discrimination Threshold Measurement

6.1.1 Method

6.1.1.1 Participants

Five participants (two male) including the author ZP participated in the experiments. The mean age was approximately 26.4 ranging from 23 to 29. All participants reported normal or corrected-to-normal vision, and had no history of neurological or visual disorders. Participants provided written informed consent and the experimental protocols were approved by the Human Ethics Committee of Bilkent University.

6.1.1.2 Stimuli and Design

The stimuli were presented on a CRT monitor (HP P1230, 22 inch, 1024 X 768 resolution). To be able to present very fine-grained contrast differences, the dynamic luminance range of the monitor is increased (14-bit luminance resolution) using a digital-to-analog converter (Bits#, Cambridge Research Systems Ltd., UK). Presentation of correct luminance values was ensured by using a 14-bit gamma-corrected gray scale lookup table prepared after measurements of every four steps in a range that is necessary for generation of our stimuli with a colorimeter (SpectroCAL, Cambridge Research Systems Ltd., UK). Participants were seated 75 cm from the monitor, and their heads were stabilized using a chin rest. Participants' responses were collected via a standard computer keyboard.

The illusory checkerboard stimulus subtended 20 by 20 degrees of visual angle. Approximate size of the context squares was 2.65 by 2.65 degrees of visual angle. Luminance of the context square was 8.17 cd/m^2. Rectified square-wave gratings weighted by two-dimensional isotropic Gaussian envelopes were superimposed on the context squares of the illusory stimulus. Contrast of the gratings was defined by Weber Contrast. Incremental and decremental gratings with frequency of 2 cpd were tested. In the experiment, contrast detection and discrimination thresholds were measured at two baseline contrasts (0 (0%) and 0.2 (20%) contrast levels), using an adaptive two-interval forced-choice (2-IFC) procedure. The baseline contrasts were tested in different sessions. At the beginning of each trial, either original checkerboard stimulus or the mirror-symmetric version of it presented randomly. Gratings were superimposed on only the right CS, which might be either darker or lighter depending on the trial, throughout a session. Each trial started with a 3000 ms illusory stimulus presentation, followed by two intervals each presented for 500 ms. Intervals were separated by a 500-ms inter-stimulus interval (ISI), the illusory stimulus remained on the screen during the ISI. A beep-sound was presented at the beginning of each interval in order to inform participants that the interval begins. In one of the two intervals randomly chosen, a standard grating with baseline contrast was presented and a test grating of slightly higher contrast than the standard grating was presented in the other interval. There was a fixation mark in the middle of two CS and participants were required to fixate on it throughout the session. Participants were asked to decide the temporal position of the grating with higher contrast (test grating) by pressing either left arrow or right arrow button in a keyboard (Figure 6.1). An auditory feedback was provided following only an incorrect response. Darker and lighter CSs were tested within the same session. Two interleaved staircases were applied for each CS independently (4 staircases in total, each containing 60 trials, 240 trials in total) in a single session. After each trial, contrast of the next test grating was decided based on the previous responses following a 1-up 3-down adaptive staircase with 0.3% contrast steps for 0%, and 0.5% contrast steps for

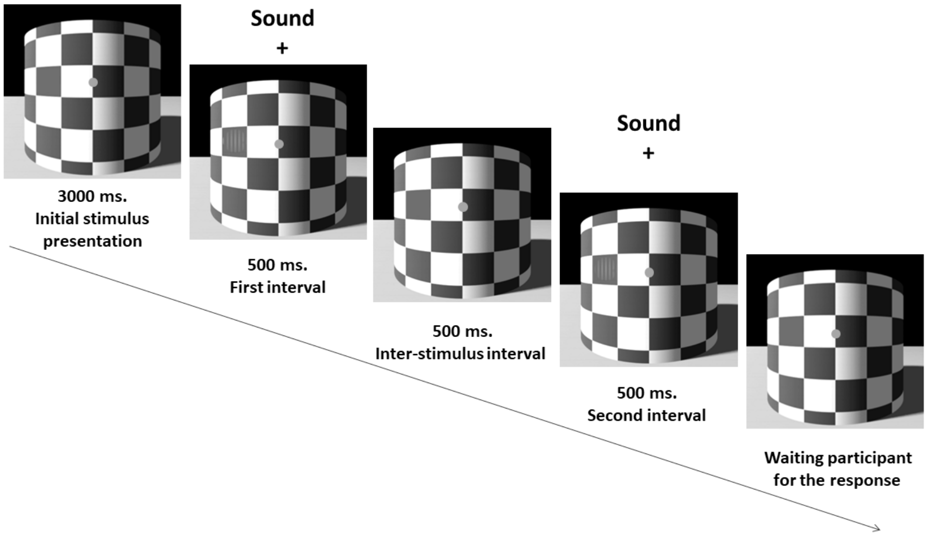

Figure 6.1: Protocol for the discrimination threshold experiment. At the beginning of each trial, either original checkerboard stimulus or the mirror-symmetric version of it presented randomly. Gratings were superimposed on only the right CS, which might be either darker or lighter depending on the trial. A beep-sound was presented at the beginning of each interval in order to inform participants that the interval begins. In one of the two intervals randomly chosen, a standard grating with baseline contrast was presented and a test grating of slightly higher contrast than the standard grating was presented in the other interval. There was a fixation mark in the middle of two CS and participants were required to fixate on it throughout the session. Participants were asked to decide the temporal position of the test grating.

20% baseline contrast. There were four conditions (2 contrast type (incremental or decremental) X 2 baseline contrast levels (0% or 20%)) in the experiment. In order to be conservative about the results, measurement of each condition was repeated three times on each participant. Therefore, observers participated in twelve experimental sessions.

6.1.1.3 Data analysis

Data were first analyzed with Palamedes toolbox to find the threshold (79% success) [60] in Octave (http://www.octave.org). Standard error of the thresholds were computed using bootstrapping. For decremental contrasts, before computing the threshold, we first converted the negative values to positive. Raw data were converted to discrimination threshold by subtracting the threshold from baseline contrast. Analyses were done using the mean of three repeats of each condition. We conducted repeated measures ANOVA with three factors (contrast type, CS, contrast level) and thresholds for different CSs were compared using a two-tailed paired-samples Student's t-test in SPSS.

6.1.2 Results

Results are shown in Figure 6.2. Also, mean proportion of correct responses averaged across participants and corresponding PFs are plotted in Figure 6.3 as a function of stimulus contrast.Similar to previous experiments, main effect of CS was statistically significant (F(1,4) = 221.8, $p < 0.001$). Mean discrimination threshold for the gratings superimposed on darker CS (M = 2.9, SEM = 0.2) was higher than that on the lighter CS (M = 2.5, SEM = 0.2). Also, main effect of contrast (F(1,4) = 32.51, $p < 0.01$) was statistically significant. Mean discrimination threshold for the gratings with 20% baseline contrast (M = 4, SEM = 0.5) was higher than that with the 0% baseline contrast (M = 1.4, SEM = 0.1) as expected considering a typical threshold-versus-contrast (TvC) curve. Furthermore, unlike previous results, main effect of contrast type was also significant (F(1,4) = 8.77, $p < 0.05$). Mean thresholds for the incremental gratings (M = 2.9, SEM = 0.3) was higher than that with the decremental gratings (M = 2.5, SEM = 0.2).

Detection threshold at 0% baseline contrast was significantly higher when gratings were superimposed on perceptually darker CSs than that on lighter CSs both for incremental (for lighter CS: M = 1.2, SEM = 0.09; for darker CS: M = 1.6, SEM = 0.1; t(4) = 8.58, $p < 0.01$) and decremental gratings (for lighter CS: M = 1.2, SEM = 0.06; for darker CS: M = 1.4, SEM = 0.08; t(4) = 7.83, $p < 0.01$). Results were similar for discrimination thresholds at 20% baseline contrast. There was a significant difference in discrimination thresholds of gratings superimposed

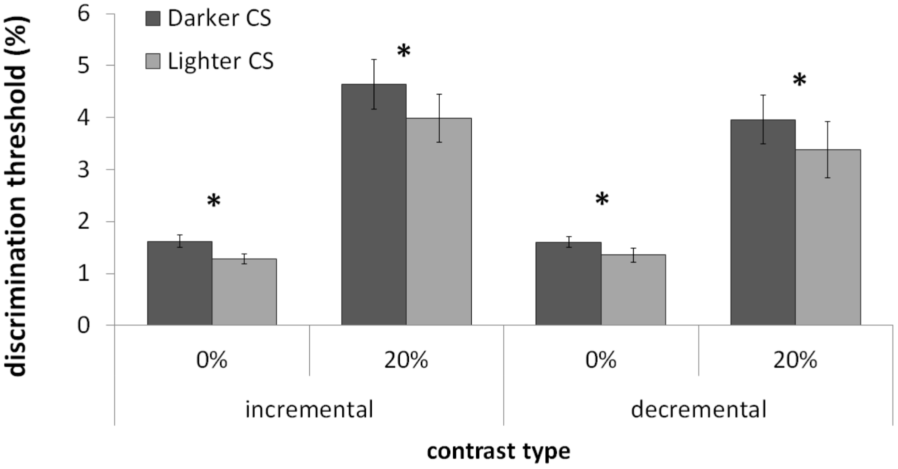

Figure 6.2: Discrimination Thresholds for the incremental and decremental gratings superimposed on either darker or lighter CSs. Here, mean of three repeats of each condition was reported. Discrimination threshold is higher when gratings are superimposed on darker CS. * $p < 0.05$. Error bars show ±1 SEM.

on lighter and darker CS both for the incremental gratings (for lighter CS: M = 3.9, SEM = 0.4; for darker CS: M = 4.6, SEM = 0.4; t(4) =3.42, $p < 0.05$) and the decremental gratings (for lighter CS: M = 3.3, SEM = 0.4; for darker CS: M = 3.9, SEM = 0.4; t(4) = 2.98, $p < 0.05$).

6.1.3 Intermediate Summary and Discussion

Results of the present experiment was consistent with our previous results (see Section 3.2 in Chapter 3). For the detection threshold of incremental and decremental gratings, a lower contrast is required in order to detect the presence of a grating when it is superimposed on perceptually lighter CS compared to those superimposed on perceptually darker CS. Also, as we predicted, the same effect was observed for discrimination threshold of incremental and decremental gratings.

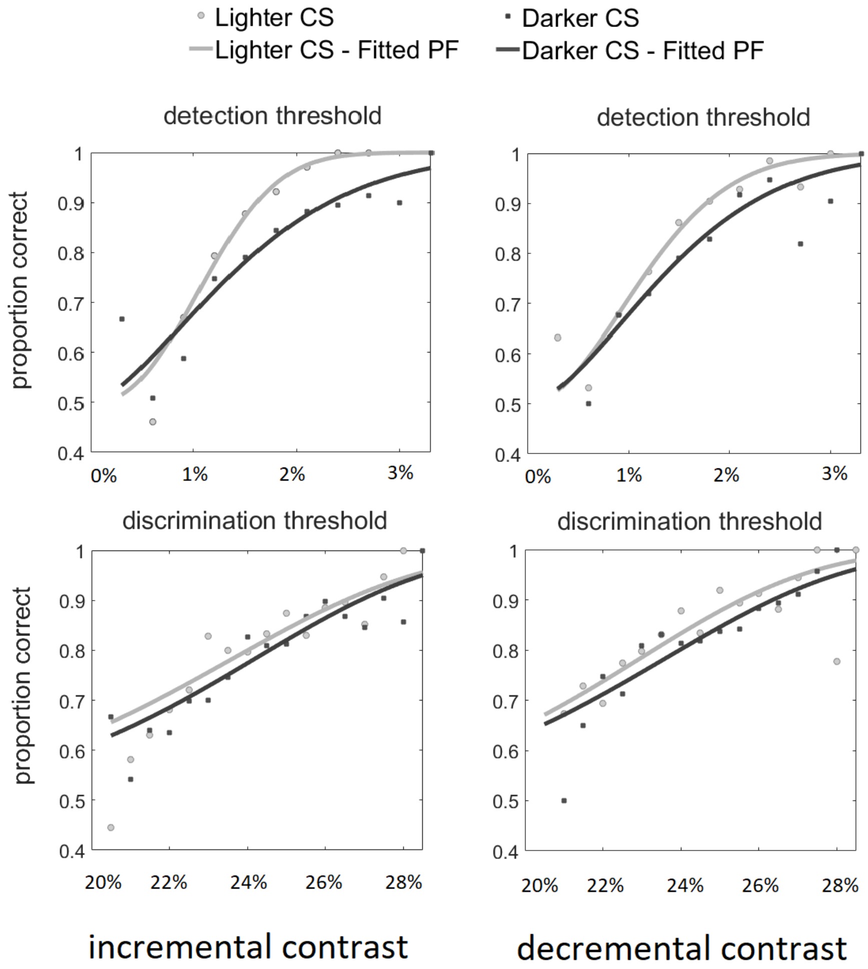

Figure 6.3: Mean proportion of correct responses averaged across participants as a function of stimulus contrast, and corresponding psychometric functions (PF).

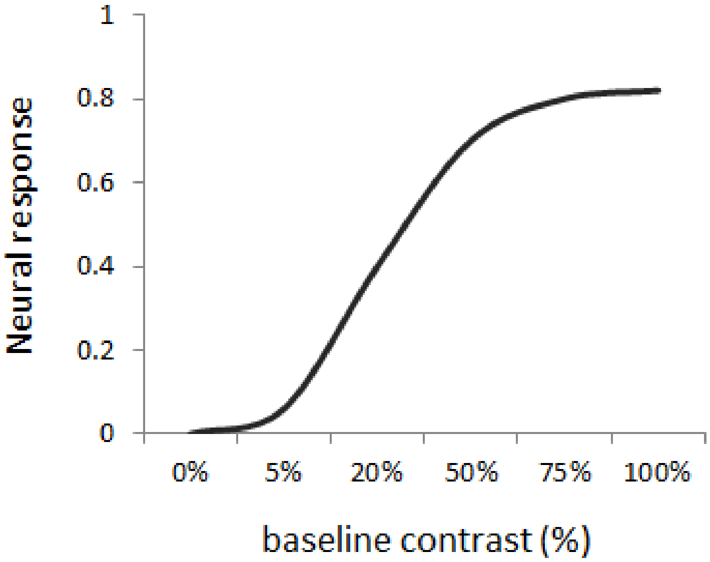

Figure 6.4: Example contrast response function (CRF). It forms a sigmoidally shaped function that expanses at low contrast levels and compresses at high contrasts where response saturates; and neural response increases relatively linearly at midrange contrast levels.

6.2 fMRI of Contrast Discrimination Measurement

Single-unit recording and human imaging data suggest that increases in stimulus contrast cause a monotonic increase in neural activity in V1 [71, 72]. However, the increase in neural activity is not linear across all ranges of contrast. It forms a sigmoidally shaped contrast response function (CRF, see Figure 6.4 for an example) that expanses at low contrast levels and compresses at high contrasts where response saturates; and neural response increases relatively linearly at midrange contrast levels [71]. Behaviorally, contrast discrimination threshold is represented as a function of baseline contrast and it is called a threshold versus contrast or a TvC curve [73, 70, 74] (see Figure 6.5 for an example). At zero baseline contrast, the minimum contrast increment that can be detected is called detection threshold. As the baseline contrast increases above zero, discrimination threshold first drops below the detection threshold; and then it increases again.

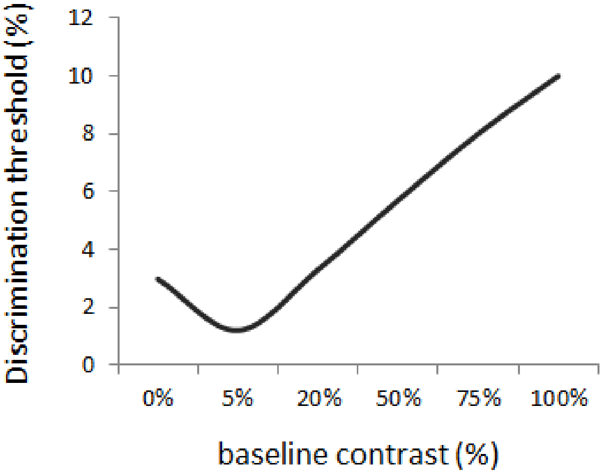

Figure 6.5: Example threshold versus contrast (TvC) curve. Behaviorally, contrast discrimination threshold is represented as a function of baseline contrast and it is called a TvC curve. At zero baseline contrast, the minimum contrast increment that can be detected is called detection threshold. As the baseline contrast increases above zero, discrimination threshold first drops below the detection threshold; and then it increases again.

Behavioral performance on discrimination is believed to be limited by neuronal signals in early visual areas [70]. In other words, in order to detect an increment in contrast behaviorally, neural activity should increase by a criterion amount. Therefore, shape of the TvC curve depends on contrast response function, and discrimination thresholds can be predicted from the inverse of the slope of CRF [70]. For example, discrimination threshold is lower at the contrast levels where slope of the CRF is steeper because neural response increases by the criterion amount with less increase in stimulus contrast. In our study, if the fMRI and the threshold data is consistent, we would expect to see steeper slopes for the CRF of both incremental and decremental gratings superimposed on lighter CSs than that of darker CS because thresholds were significantly lower for those gratings superimposed on lighter CSs. However, instead of the threshold results, if our fMRI result is consistent with the appearance results, we would expect to see larger BOLD response increases only for the incremental gratings superimposed on lighter CSs, but not for decremental gratings because perceived contrast significantly increased only for the incremental gratings superimposed on lighter CSs (see Figure 6.6 for expected results). In order to compute the slope at the contrast

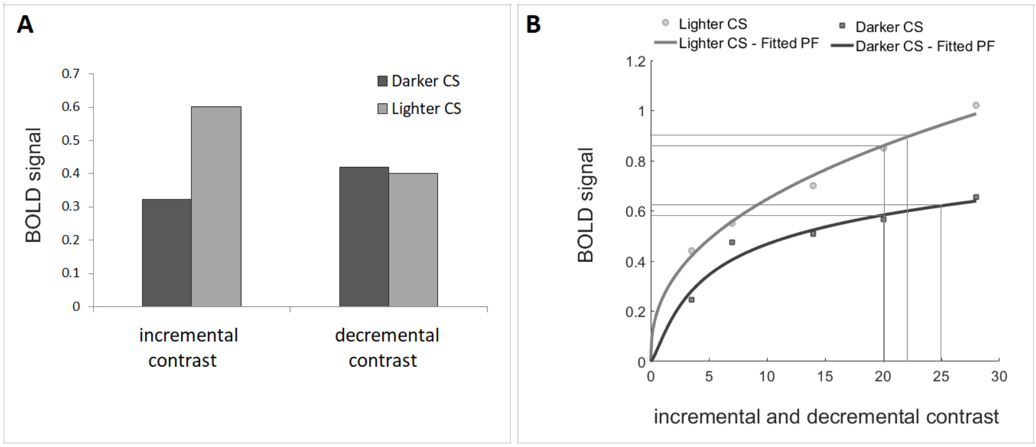

Figure 6.6: Expected fMRI results based on the appearance and threshold results. (A) In a case that BOLD activity in a cortical area is related to contrast appearance we would expect to see different patterns for incremental and decremental gratings. BOLD signal should be higher for the incremental gratings on lighter CS than that of superimposed on darker CS, and it should be similar for decremental gratings superimposed either on lighter CS or darker CS. (B) In a case that BOLD activity in a cortical area is related to thresholds, we would expect to see steeper slope of CRF for the grating superimposed on the lighter CS both for incremental and decremental grating conditions. Thin lines show the relationship between stimulus contrast (on the x axis) and criterion amount increase (on the y axis). For instance, for the 20% baseline contrast, contrast of a grating superimposed on darker CS should be higher than that of superimposed on lighter CS in order to evoke the neural response increase by criterion amount.

levels we tested in the behavioral experiments, we collected data from five contrast levels (3.5%, 7%, 14% 20% and 28%) in the fMRI study. Also, we replicated appearance experiments in the scanner to ensure that the stimulus conditions were identical for behavioral and fMRI experiments and context-dependent lightness effect is still observed under the conditions in the scanner.

6.2.1 Behavioral Adjustment Experiment in the Scanner

6.2.1.1 Method

6.2.1.1.1 Participants Five participants (two male) including the author ZP participated in the experiment. All five had previously participated in the behavioral discrimination threshold measurement experiments (Section 6.1).

6.2.1.1.2 Stimuli and Design Visual stimuli were presented on a MR-compatible LCD monitor (TELEMED, 32 inch, 1920 X 1080 resolution) that was viewed by participants through a mirror located above their eyes inside the scanner. The viewing distance was 170 cm. The monitor was calibrated using a SpectroCAL (Cambridge Research Systems Ltd.) colorimeter.

For this experiment, we replicated our previous adjustment experiment while participants were lying in the scanner. We tested one contrast and one frequency level (20% incremental or decremental contrast, 2 cpd spatial frequency). Participants' task was to perceptually adjust the contrast of a match grating to match that of the standard grating. Differently from our previous experiments, the standard grating was placed on one of the CSs and the match grating was placed on the other CS. The approximate size of the grating was 1.6 degree. There was a fixation mark between the two CSs. Participants were asked to fixate the fixation mark while performing the adjustment task. Contrast of the rectified square-wave gratings were defined by Weber Contrast. The tested incremental and decremental contrast level was 0.2 and -0.2, respectively. Adjustment was done in 0.02 steps using the buttons of an MRI-compatible response pad. We used the version of the checkerboard stimulus in which CS luminance was 13.82 cd/m^2. Checkerboard stimuli were presented on a gray background whose luminance was 24.39 cd/m^2. In each trial the contrast of the match had the same contrast polarity as the standard and its initial contrast was determined randomly at the start of each trial. Each session contained 10 trials with 5 repetitions for every combination of conditions (1 contrast level X 2 CS positions X 5 repetitions). Incremental and

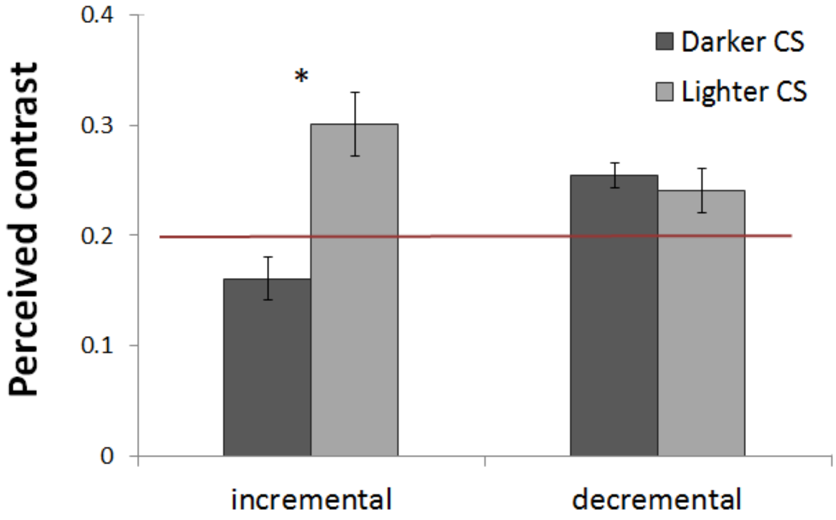

Figure 6.7: Mean settings in the perceived contrast experiment in the scanner. Red horizontal line corresponds to the actual contrast. * $p < 0.05$. Error bars represent ±1 SEM.

decremental contrast patterns were tested in different blocks.

6.2.1.1.3 Data Analysis Analyses were performed on averaged perceived contrast scores. First, a repeated-measures ANOVA was conducted in order to test two factors: contrast type (two levels: incremental, decremental), and CS (two levels: darker, lighter). Also, we conducted two-tailed paired-samples Student's t-test in SPSS in order to test whether perceived contrasts of gratings superimposed on either darker or lighter CSs are significantly different. For decremental contrasts, before computing the mean perceived contrast, we first converted the levels to positive values.

6.2.1.2 Results

Behavioral results in the scanner are shown in Figure 6.7. The repeated-measures ANOVA results showed that main effect of contrast type ($F(1,4) = 0.34$, $p > 0.05$) and main effect of CS ($F(1,4) = 2.97$, $p > 0.05$) was not statistically significant. However, the interaction between contrast type and CS ($F(1,4) = 18.36$, $p < 0.05$)

was significant. For the incremental grating condition, perceived contrast of gratings superimposed on lighter CSs was higher than those superimposed on darker CS (t(4)= 3.34, $p < 0.05$). For the decremental grating condition, the difference was not significant (t(4)= 0.33, $p > 0.05$). In this experiment, consistent with our previous adjustment experiments, we found that perceived contrast increased with context-dependent lightness of the background for incremental gratings, but not for decremental gratings.

6.2.2 fMRI Experiment

6.2.2.1 Method

6.2.2.1.1 Participants Five participants (two male) including the author ZP participated in the experiment. All five participants had also participated in the behavioral discrimination threshold measurement experiments and behavioral adjustment experiments in the scanner.

6.2.2.1.2 Stimuli and Design Visual stimuli were presented on a MR-compatible LCD monitor (TELEMED, 32 inch, 1920 X 1080 resolution) that was viewed by participants through a mirror located above their eyes inside the scanner. The viewing distance was 170 cm. The monitor was calibrated using a SpectroCAL (Cambridge Research Systems Ltd.) colorimeter.

The illusory checkerboard stimulus was used in the experiments. Photometrically identical rectified square-wave gratings weighted by two-dimensional isotropic Gaussian envelopes were superimposed on both CSs simultaneously. 3.5%, 7%, 14%, 20% and 28% incremental and decremental contrast levels, defined by Weber Contrast, were tested in different runs. In the first 24 seconds subjects viewed only the illusory stimulus without gratings. In a block design, subjects viewed five 12-second alternating blocks of two conditions. In the first condition, gratings were presented (experimental blocks). Experimental blocks were separated by control blocks where gratings were absent on the illusory checkerboard stimulus. In all blocks, subjects viewed a dynamical fixation mark whose color is alternating between black, red and green. Participants were asked to fixate the fixation mark, and they were required to report the changes in its color by pressing the response pad. Gratings were flickering at 4 Hz to avoid adaptation of neurons. Five fMRI scans for different contrast levels times two for different contrast types were applied. Each condition was repeated two times using the mirror-symmetric versions of the illusory stimulus. As a result, there were twenty fMRI scans in the experiment. Also, the experiment included an anatomical scan, and two functional region of interest (ROI) localization scans.

6.2.2.1.3 Region of Interest (ROI) localization Retinotopic visual areas were defined in a different session based on responses to rotating wedge and expanding rings of flickering black and white checks, using the standard phase-encoded retinotopic mapping methods (see an example in Figure 5.3) [68, 69].

Functional ROIs were identified in two different scans within the main experimental session. One scan was conducted using incremental and the other was conducted using decremental contrast gratings. Cortical areas corresponding to the location of gratings on CSs were functionally localized by conventional methods in which subjects viewed flickering gratings on a trapezoid-shaped background whose luminance, size and locations were exactly the same as the CSs (see Figure 5.4). Gratings with 20% contrast and 2 cpd frequency levels were used. First, the trapezoid-shaped left and right backgrounds were presented during 24 seconds as an initial blank period. Later, in an experimental block, flickering gratings were presented for 12 seconds on both left and right backgrounds simultaneously. The experimental block was repeated for five times in a scan, separated by 12 seconds control blocks. In control blocks there were no gratings on the backgrounds. In this scan, participants were required to respond to changes in color of the fixation mark.

6.2.2.1.4 MRI data acquisition Scanning protocols were the same with the previous fMRI experiment (see Section 5.2.1.4).

6.2.2.1.5 fMRI data processing and analyses MRI data were preprocessed and ROIs were defined as it is explained in Section 5.2.1.5. ROIs defined by the incremental grating ROI scan was used to analyze the data in the incremental grating conditions and ROIs defined by the decremental grating ROI scan was used to analyze the data in the decremental grating conditions. For each fMRI scan, the time course of BOLD responses was extracted by averaging the data across all the voxels within the pre-defined ROIs in V1, V2, V3, and V4; and then normalized by the mean BOLD signal across the scan. Next trial-onset locked event-related averaging was performed, and the average response between 8 and 12s of control condition (0-4 secs. before the stimulus onset) was subtracted from the average response from forth to sixth volume (between 6 and 12s after the stimulus onset) of the experimental block as the average response for further analyses. Data was analyzed in two different ways in order to compare the fMRI results with the appearance and threshold results separately. To see whether fMRI and appearance results are consistent repeated-measures ANOVA was conducted using average response scores. Three factors, contrast type (two levels: incremental, decremental), contrast level (five levels: 3.5%, 7%, 14%, 20%, 28%), and CS (two levels: perceived darker, lighter) were tested. Additionally, a two-tailed paired-samples Student's t-test was applied in SPSS to the data averaged across contrast levels corresponding to darker and lighter CSs for incremental and decremental condition separately. If the fMRI and the appearance data is consistent, we would expect to see larger BOLD response increases for the conditions where perceived contrast increased significantly. In order to see whether fMRI and threshold results are consistent we first fitted a CRF to the fMRI data averaged across participants. We used the following equation suggested by Boynton et al. [70] to fit CRF:

$$\hat{R}(C) = \alpha \frac{C^{p+q}}{C^q + \sigma^q}, \tag{6.1}$$

where, R and C correspond to response and stimulus contrast, respectively. The value of other symbols defines the shape of the function. In order to fit the function to the averaged fMRI data we performed a numerical search to minimize error using the weighted least-squares error function below:

$$X^2 = \sum_i \frac{[\hat{R}_i - R_i]^2}{\sigma_i^2}, \tag{6.2}$$

where $\hat{R}$ and R are the predicted and measured responses to the i*th* scan (thus the i*th* contrast level), respectively. Standard error of the mean for each contrast level was computed considering the variance across participants and this value is defined as a variance in the data by σ_i^2 in the equation. After we fit the CRF, we computed the slopes at 0% and 20% contrast levels. If the fMRI and the threshold data is consistent, We would expect to see steeper slopes for the conditions where the thresholds are significantly lower. In order to compute the standard errors of the slopes, we bootstrapped the data and computed estimated standard errors.

6.2.2.2 Results

We could define the functional ROIs for four out of five participants. Therefore, further analyses are conducted using data from four participants. Below, the results were compared with the behavioral appearance and threshold results separately.

6.2.2.2.1 Are the fMRI results consistent with appearance results?

6.2.2.2.1.1 Activity within pre-defined functional ROI in V1 Results at the 20% contrast level are shown in Figure 6.8 (top left). Analyses showed that main effect of CS (F(1,3)=19.47, $p < 0.05$) was statistically significant. Main effect of contrast was also significant (F(4,12)=4.97, $p < 0.05$). However, main effect of contrast type was not significant (F(1,3)=1.53, $p > 0.05$). Also, there was no significant interaction. Two-tailed paired-samples Student's t-test results showed that for the decremental grating condition, the BOLD response was larger when the grating was superimposed on perceptually lighter CS (t(3)=4.84, $p < 0.05$). The same pattern was observed for the incremental grating condition. The BOLD response tended to be larger when the grating was superimposed on the lighter CS but the difference was not statistically significant (t(3)=2.85, p = 0.065). Results showed that for both contrast types, BOLD response in V1 tended to increase when identical gratings were superimposed on the perceptually

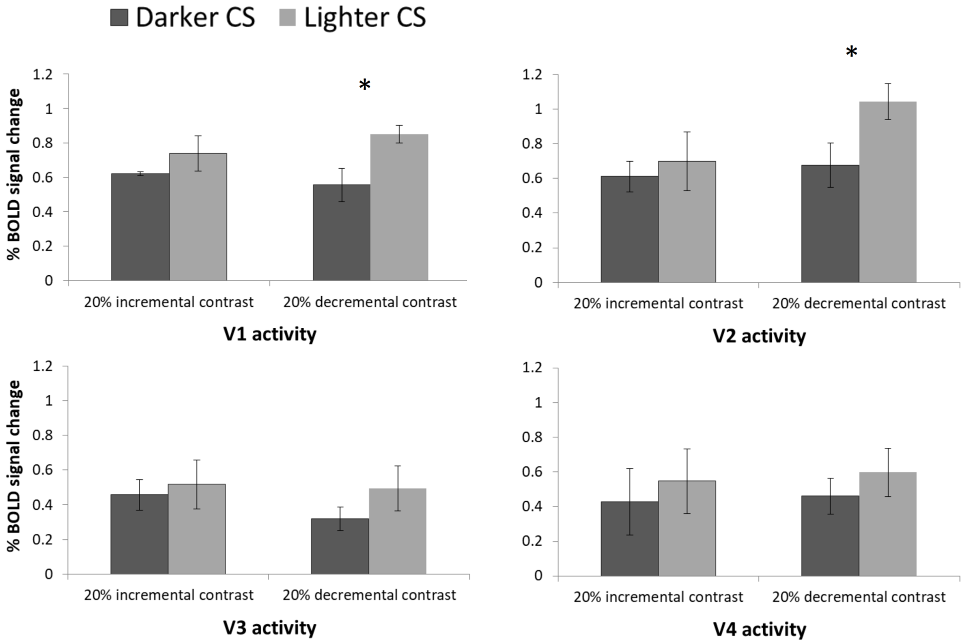

Figure 6.8: Mean BOLD signal change for 20% incremental and decremental contrast in V1, V2, V3 and V4. BOLD signal amplitude is higher both for incremental and decremental gratings superimposed on lighter CS. * $p < 0.05$. Error bars represent ±1 SEM.

lighter CS. BOLD activity changed significantly depending on the CS for decremental gratings. The same pattern was observed for incremental gratings but the difference was not statistically significant. Overall, results showed that activity in V1 was not completely consistent with the context-dependent lightness effect on perceived contrast.

6.2.2.2.1.2 Activity within pre-defined functional ROI in V2 Results at the 20% contrast level are shown in Figure 6.8 (top right). Analyses showed that main effect of CS (F(1,3)=23.38, $p < 0.05$) was statistically significant. Main effect of contrast was also significant (F(4,12)=8.7, $p < 0.05$). However, main effect of contrast type was not significant (F(1,3)=1.98, $p > 0.05$). Also, there was no significant interaction. Two-tailed paired-samples Student's t-test results showed that for the decremental grating condition, the BOLD response was increased when the grating was superimposed on perceptually lighter

CS (t(3)=4.009, $p < 0.05$). The same pattern was observed for the incremental grating condition, that is the BOLD response tended to be larger when the grating was superimposed on lighter CS but the difference was not statistically significant (t(3)=0.85, $p > 0.05$). Results showed that activity pattern was very similar to those of V1. Results showed that activity in V1 was not completely consistent with the context-dependent lightness effect on perceived contrast.

6.2.2.2.1.3 Activity within pre-defined functional ROI in V3 Results at the 20% contrast level are shown in Figure 6.8 (bottom left). A similar trend was observed in V3, that is the BOLD response tended to increase when the grating was superimposed on perceptually lighter CS. However, main effect of CS (F(1,3)=6.57, $p = 0.083$) was not significant. Also, main effect of contrast type was not significant (F(1,3) =1.91, $p > 0.05$). However, main effect of contrast was significant (F(4,12) =7.59, $p < 0.05$). There was no significant interaction. Two-tailed paired-samples Student's t-test results showed that both for the decremental grating condition (t(3)=1.78, $p > 0.05$) and for the incremental grating condition (t(3)= 3.06, p = 0.055), BOLD activity did not change significantly depending on the CS. Results showed that activity in V3 was not consistent with the context-dependent lightness effect.

6.2.2.2.1.4 Activity within pre-defined functional ROI in V4 Results at the 20% contrast level are shown in Figure 6.8 (bottom right). A similar trend was observed in V4, that is the BOLD response tended to increase when the grating was superimposed on perceptually lighter CS. However, main effect of CS (F(1,3)=1.62, $p > 0.05$) and main effect of contrast type was not significant (F(1,3) =0.89, $p > 0.05$). However, main effect of contrast was significant (F(4,12) =5.11, $p < 0.05$). Also, there was no significant interaction. Two-tailed paired-samples Student's t-test results showed that both for the decremental grating condition (t(3)=1.23, $p > 0.05$) and for the incremental grating condition (t(3)= 1.2, $p > 0.05$), BOLD response did not change significantly depending on the CS. Results showed that activity in V4 was not consistent with the context-dependent lightness effect.

6.2.2.2.2 Are the fMRI results consistent with threshold results? In order to see whether fMRI and threshold results are consistent we first fitted CRF to the mean fMRI data averaged across participants and we computed standard errors using bootstrapping. Mean BOLD signal amplitude in V1,V2, V3, and V4 as a function of contrast and fitted CRFs to the actual data is plotted in Figure 6.9. In order to compare the BOLD activity and detection threshold performance we computed the slope CRF between 0% and 1% contrast levels and those slopes were plotted in Figure 6.10 across V1, V2, V3, and V4. BOLD activity pattern in all visual areas are consistent with the behavioral performance that detection thresholds were lower for the conditions where the slope is steeper.

Discrimination threshold at 20% baseline contrast (note that this is the value we tested in the discrimination threshold experiments) performance should be predicted from the slope of CRF at 20% contrast level and those slopes were plotted in Figure 6.11 across V1, V2, V3, and V4. For the incremental gratings, BOLD activity pattern in V2, V3 and V4 was consistent with the discrimination threshold performance. For the decremental gratings, BOLD activity pattern was not consistent with the discrimination threshold performance in any visual area.

6.2.3 Intermediate Summary and Discussion

Results of the present fMRI experiment showed that BOLD response tended to increase for the gratings superimposed on the perceived lighter CS more than those superimposed on the darker CS. However, for most of the conditions this difference did not reach to the significance level even for the conditions we could observe significant differences in our previous fMRI experiment (see Chapter 5). We believe that this is mainly caused by the limited number of participants we have in the present study. Still, inspecting the patterns in results, we see that the fMRI activity is not consistent with the appearance results. Perceived contrast was higher for the incremental gratings superimposed on lighter CSs compared to those superimposed on darker CSs in the appearance experiment. However, perceived contrast of decremental gratings was not affected by the context-dependent

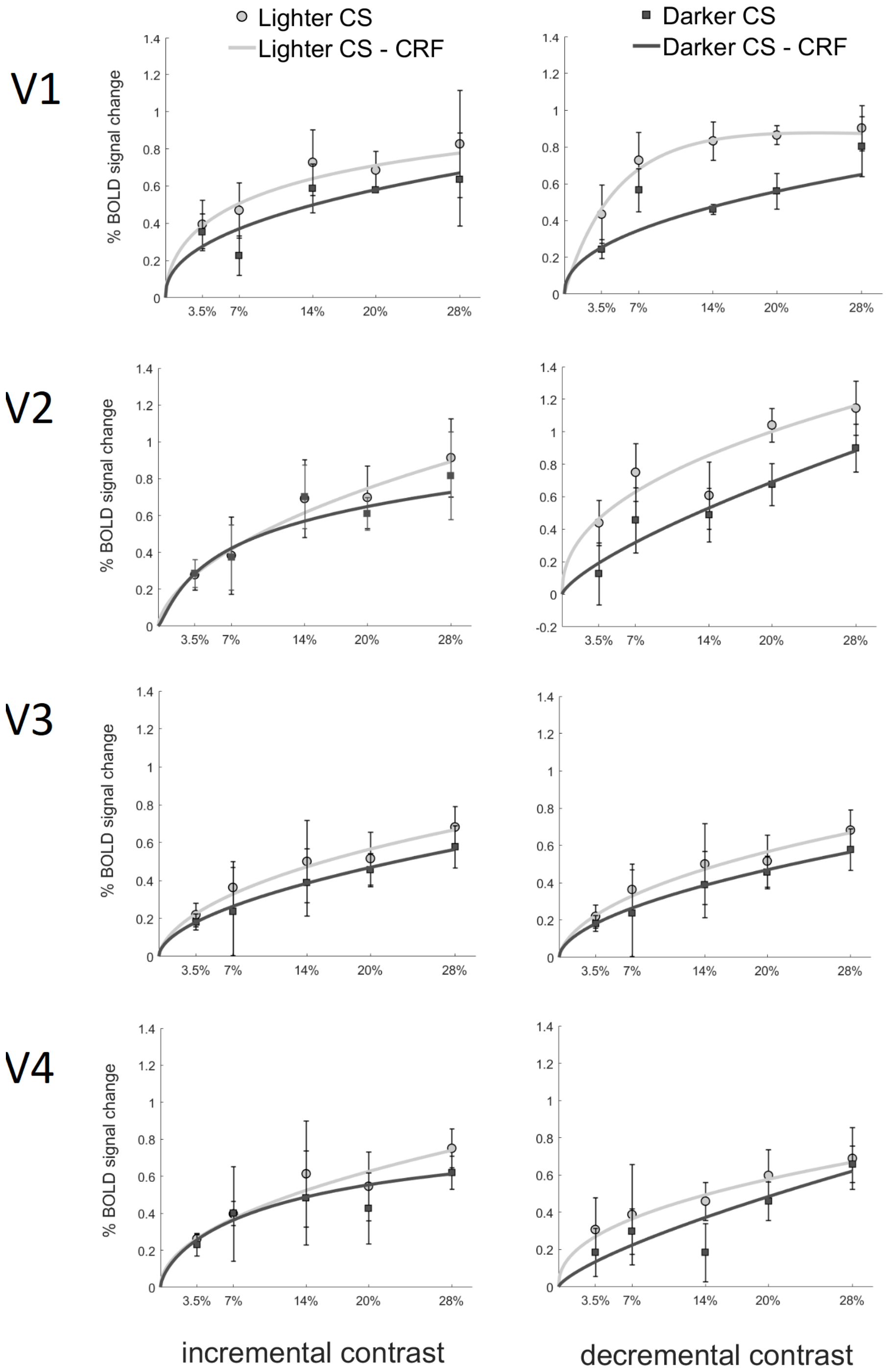

Figure 6.9: Mean BOLD response amplitude in V1, V2, V3, and V4 as a function of contrast and fitted CRFs to the actual data. BOLD response change tended to be larger for the gratings superimposed on the lighter CS for the most of the conditions we tested in all visual areas. Error bars represent ±1 SEM.

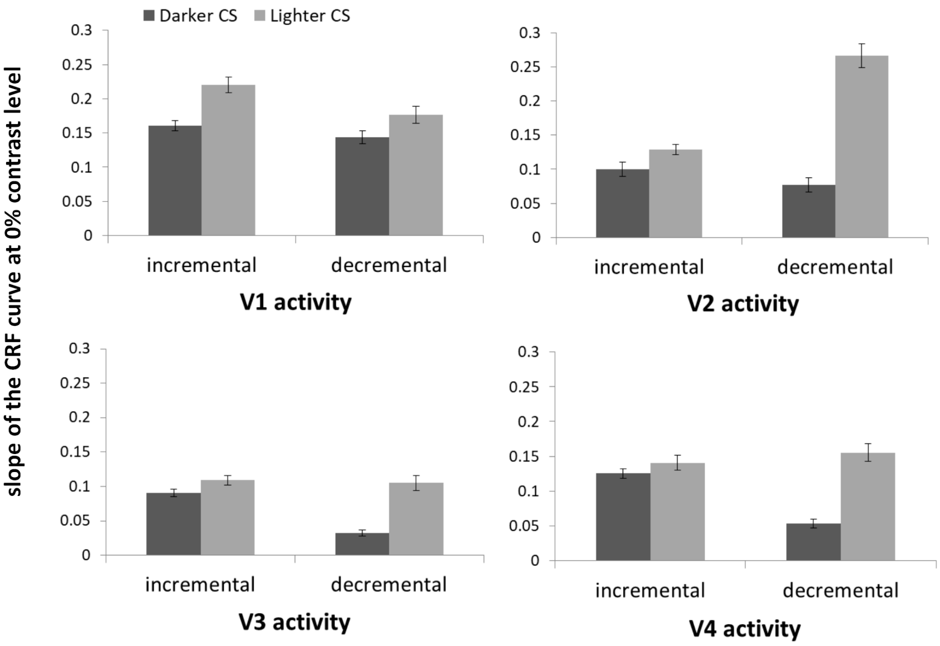

Figure 6.10: Slope of the CRF curve between 0% and 1% contrast level in V1, V2, V3, and V4. CRF was fitted to the mean fMRI data averaged across participants. According to the recent models of contrast processing, slopes should be higher at the points that detection threshold is lower. Results are consistent with this expectation in all visual areas. Error bars represent ±1 SEM obtained by bootstrapping.

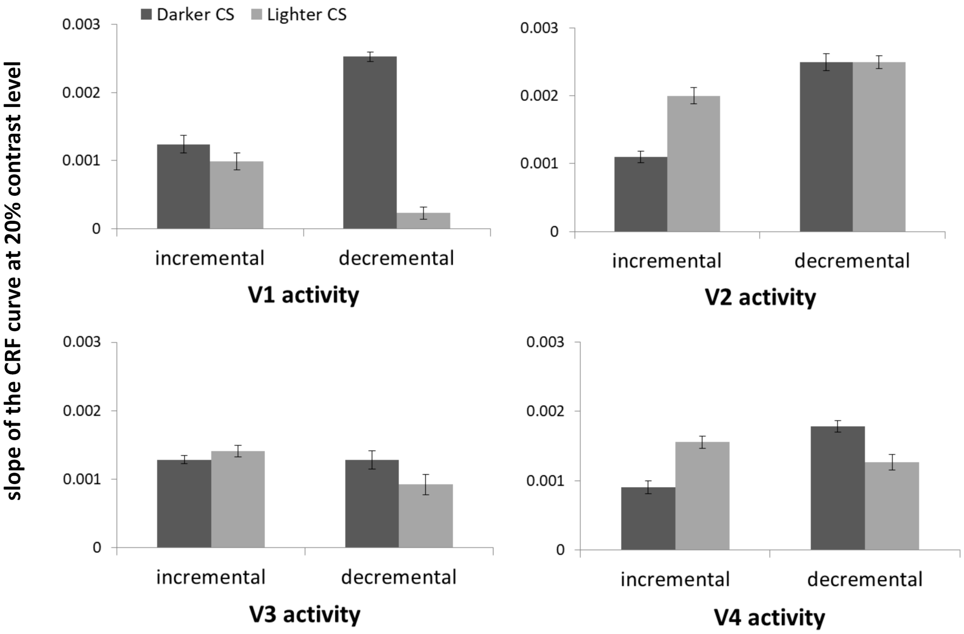

Figure 6.11: Slope of the CRF curve at 20% contrast level in V1, V2, V3, and V4. CRF was fitted to the mean fMRI data averaged across participants. According to the recent models of contrast processing, BOLD activity slopes should be higher at the points that discrimination threshold is lower. For the incremental gratings, the BOLD activity pattern in V2, V3 and V4 is in line with this expectation. However, for the decremental gratings the activity pattern does not agree with the expectation. Error bars represent ±1 SEM obtained by bootstrapping.

lightness. Although there is no significant behavioral context-dependent lightness effect for the decremental grating conditions, fMRI results indicated significant BOLD increase when the gratings were superimposed on lighter CSs than those superimposed on darker CSs. Our fMRI results are not completely consistent with the threshold results either considering the contrast processing models in literature [e.g., 70]. According to the recent models, thresholds should be predicted from the inverse of the slope of CRF, and lower threshold scores should be observed where the fMRI data has steeper slopes. Therefore, in our experiment since we observed lower detection and discrimination thresholds for the gratings superimposed on lighter CS, we also expected to see steeper slopes in the fMRI data for those gratings at least at the contrast levels we measured behaviorally. The relationship between the fMRI data and the detection threshold data was consistent with this expectation. However, we could not see such a pattern for the fMRI and the discrimination threshold data. Still, variation in the fMRI activity with varying contrast links better with the thresholds than the appearance results because fMRI data at least correlates well with the detection threshold data. Therefore, we believe that this study offers a neural evidence for dissociation between the mechanisms underlying detection (threshold) and identification (appearance) measures [9]. It should also be noted that the reason why we could not see the expected relationship between fMRI and discrimination threshold data might be due to the insufficiency of the recent contrast processing models in order to explain the contrast processing in context. Therefore, we would need to develop new models. In addition to the slope of CRF, absolute or perceived values of contrast might also contribute to the contrast thresholds. Therefore, these models should be revisited again and tested in context, too.

Chapter 7

Discussion

In this thesis work, I have investigated how contrast detection and identification of rectified square-wave gratings is affected by the context-dependent lightness of its background using psychophysical and functional magnetic resonance imaging (fMRI) methodologies. In behavioral experiments, we modeled detection and identification by threshold tasks and appearance tasks, respectively [9]. In our experiments we used an illusory checkerboard stimulus in which two equiluminant "context squares" (CSs) appeared different in lightness (Figure 2.1). First, in a behavioral experiment we ensured that the stimulus had the desired lightness effect on all participants. Later, in a series of experiments we measured the contrast appearance of incremental and decremental rectified square-wave gratings superimposed on the CSs. We found that perceived contrast increased with context-dependent lightness of the background for incremental gratings, but not for decremental gratings. More specifically, when identical incremental gratings are superimposed on equiluminant backgrounds, the one on the perceptually lighter background appeared to have higher contrast. In this experiment, we investigated the appearance of gratings, not their detection or discrimination thresholds. Hillis and Brainard [9] previously showed that detection and identification of incremental elliptical patches in complex scenes similar to ours were mediated by different mechanisms. Thus, after showing the effect of context-dependent lightness on perceived contrast, in the next experiment, we investigated how context-dependent lightness affects contrast detection and discrimination thresholds using both the illusory checkerboard stimulus and a typical simultaneous brightness contrast stimulus (Figure 4.1). We first conducted detection threshold experiments. For the experiments we used the illusory checkerboard stimulus, we found that contrast detection threshold was higher when gratings were superimposed on the equiluminant but perceptually darker backgrounds. Results were partly consistent with the previous appearance experiments. Lower appearance experience cohered with the higher detection threshold. However, differently from appearance judgments, context-dependent lightness affected the detection thresholds of both incremental and decremental gratings.

Overall, our behavioral results are consistent with previous studies which showed that contrast of visual patterns in simple scenes, such as Gabor patches on a uniform background vary with their mean or background luminance [e.g., 7, 59, 15, 54]. Here we show that the effect is not limited to the background luminance but extends to context-dependent lightness. Moreover, in our study we show that even when there is no physical difference between the patterns there is still an effect of background lightness on contrast perception. Comparing physically identical patterns circumvents nonlinearities and confounds that might in principle be introduced by physical changes.

Surprisingly, context-dependent lightness of the background affected the perceived contrast of incremental gratings but not decremental ones. On the other hand, it affected the contrast detection and discrimination thresholds of both incremental and decremental gratings. Processing differences between positive and negative local contrast has been reported before in literature both by behavioral and neuronal studies [e.g., 43, 44, 45, 46, 47, 51, 52]. For example, it has been shown that detection threshold of decrement is lower than that of increment particularly when the background luminance is low [e.g., 49, 75, 50]. The light-dark asymmetry is also incorporated in some models of brightness [e.g., 76, 77]. Yeh, Xing, and Shapley [78] found that single-unit activity of V1 neurons was stronger for decrements than increments. In a human fMRI study stronger BOLD signal in V1 was reported in response to negative contrast stimuli compared to positive contrast ones [79]. Komban et al. [80] showed that dark targets are perceived faster and more accurately than light targets at suprathreshold levels on noisy backgrounds and argued that this difference indicates that greater neuronal resources are devoted to process decremental patterns in the early visual pathway. Therefore, the asymmetry found in our study could be the consequence of differentiation in the processing of positive and negative contrast by the visual system, starting from the retinal ganglion cells [81]. Note that, it is also possible that any effect of luminance or context-dependent lightness on perceived contrast of decremental patterns could have gone undetected in our experiments because of limited range of background luminances and lightnesses studied. Particularly for the isolated patches there was a trend for the effect of luminance on perceived contrast that did not reach a statistically significant level. At the moment, we do not have any explanation for the asymmetry between perceived contrast of incremental and decremental gratings. Why and how patterns presented on higher lightness, as well as luminance backgrounds should appear to have higher contrast? Likewise, why should the visual system rely more on the photometric contrast when it comes to appearance of decremental patterns? This could have adaptive advantages considering the statistics of natural scenes [82]. For example, measuring local contrast values [83] showed that negative polarity noise has a wider distribution of local contrast values than positive polarity noise. Still, asymmetries between positive and negative contrast patterns at the appearance experiments coheres with the findings in the literature. However, these findings are insufficient to explain why context-dependent lightness affects decremental gratings at the detection level but not at the identification level. A possible explanation is going to be addressed below considering the findings of the fMRI experiments.

After showing the context-dependent lightness effect both at the detection and identification levels, we conducted fMRI experiments in order to investigate the underlying neural mechanisms. In a block design, we superimposed identical flickering gratings simultaneously on perceptually darker and lighter CSs. We tested both incremental and decremental contrast patterns and showed that when identical gratings are superimposed on equiluminant backgrounds, the one on the perceptually lighter background elicited higher BOLD activity at all conditions we tested including incremental and decremental patterns. Several neuronal mechanisms could potentially account for our findings. Our behavioral and fMRI results consistently demonstrate that contrast perception is affected by visual context. These results indicate that contrast is not preserved as it computed in the retina. It is possible that in complex scenes perceived contrast is determined at a later stage and in a higher cortical area in the hierarchy of the visual system, after lightness is computed based on global information. Alternatively, perceived contrast could be determined in earlier areas, for example in V1, after receiving feedback about context-dependent lightness. The latter is plausible given fMRI results in literature showing context-dependent lightness related activity in early visual areas [e.g., 84]. Besides, BOLD activity we observed in V1 correlates with the perceptual context-dependent lightness effect on contrast. Therefore, our results support that feedback mechanisms are involved in the process of contrast computation (see Figure 7.1). Still, because of the limited temporal resolution of BOLD signal [85], we cannot clearly show the direction of information flow with the methods we used in the fMRI data analysis. Therefore, applying alternative analysis methods to the data that can show the functional connectivity and the direction of the information flow between cortical areas like dynamic causal modelling [86] would be beneficial to see the effect of feedback interactions better in future studies. In yet another alternative, the perceived contrast could be influenced directly by the context without lightness mediating the effect.

Our fMRI results highlighted an interesting relationship between behavioral and neural data. Namely, fMRI results correlated better with the threshold results than the appearance results. For the incremental gratings, higher context-dependent lightness led to a higher perceived contrast, lower detection and discrimination thresholds and higher BOLD signal in V1. For the decremental gratings, higher context-dependent lightness led to lower detection and discrimination thresholds and higher BOLD signal in V1 whereas it did not affect the perceived contrast. The reason that our BOLD results correlate better with threshold

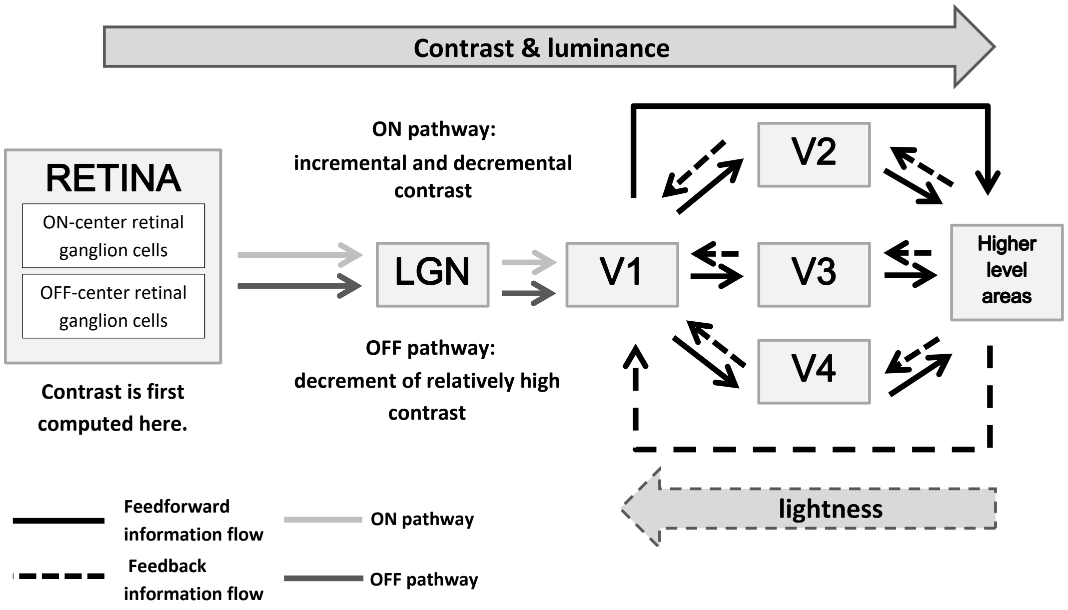

Figure 7.1: Schematic illustration of how contrast is computed in the brain based on the results of this study. There are feed-forward (also called bottom-up) and feedback pathways (also called top-down) between cortical areas in the brain. Information coming from the retina is usually transmitted to LGN and then primary visual cortex, V1, through feed-forward pathways. From V1, visual information is sent to the extra-striate cortex (V2,V3, and V4) and other higher level cortical areas. Feed-forward pathway is usually driven by sensory input. For instance, incremental and decremental contrast information is first computed in the retina and transmitted to visual cortex through ON and OFF feed-forward retinal pathways. ON pathway responds to both increment and decrement of low contrasts, whereas OFF pathway responds only to a decrement of relatively high contrast [81]. Also, ON pathway allow better intensity discrimination compared with the OFF pathway responses near threshold [87]. In addition to the feed-forward information processing of sensory input, extra-striate cortex and other higher level cortical areas send visual information which is usually driven by visual context and higher level cognitive mechanisms such as attention, and expectation to earlier visual areas through feedback pathway [88]. BOLD activity we observed in earlier visual areas including V1 correlates better with the perceptual context-dependent lightness effect than the sensory input. Therefore, contrast could be determined in earlier visual areas, after receiving feedback about context-dependent lightness.

measures than the appearance measures might be the presence of different mechanisms that mediate these tasks in the brain as Hillis and Brainard [9] showed behaviorally. Therefore, this unexpected correlation we have seen might be a neural evidence for the dissociation between underlying mechanisms of detection and identification. In order to investigate this further, we conducted additional threshold and fMRI experiments.

In the threshold experiment, we tested detection and discrimination performance and could see the effect of context-dependent lightness on both. Later, we collected fMRI data at different contrast levels. If BOLD activity in a cortical area is related to perceived contrast we would expect to see different patterns for incremental and decremental gratings. For incremental gratings BOLD signal change would be higher when gratings are superimposed on lighter CS than those superimposed on darker CS. For decremental gratings BOLD signal would not change depending on the background lightness of gratings. If the activity is related to thresholds, we would expect to see higher signal change between the two consecutive contrast levels (slope) both for incremental and decremental gratings superimposed on the lighter CS [70]. However, results were not completely in agreement with our hypothesis. Results showed that both incremental and decremental gratings superimposed on lighter CS elicited higher BOLD signal than those superimposed on darker CS. Therefore, BOLD activity was not really consistent with the appearance performance. However, the corresponding BOLD activity did not correlate well with the behavioral threshold performance either. Variation in BOLD activity with varying contrast linked well with the detection threshold performance, but it was completely unrelated to the discrimination threshold performance. Recent theories that explains the link between behavioral performance and neural activation of contrast discrimination only take into account the slope of the BOLD change [70]. However, this might be insufficient to explain the contrast processing especially for the situations that the contrast pattern is in context. In addition to the slope of CRF, absolute or perceived values of contrast might also contribute to the contrast thresholds. Therefore, these models should be tested in context, too.

Previously it has been shown that lightness of incremental elliptic targets was affected by the context-dependent lightness of their otherwise equiluminant backgrounds [9, 34, 36]. Could our results be simply explained by a purely lightness-based contrast mechanism, in which first the lightness of each pixel is estimated, and based on this the contrast is computed? Results of our control experiment do not support this possibility. The contrast of incremental gratings computed mathematically based on participants' lightness estimates were extremely different than their perceived contrasts directly measured. Our results also highlight that simply keeping photometric contrast constant does not guarantee the same for the perceived contrast and contrast threshold. This is often overlooked in lightness literature, and in some studies perceived contrast may have led to the reported lightness effects [e.g., 9, 34, 36].

The BOLD signal increase we demonstrated for the gratings superimposed on perceptually lighter CS might also be attributed to higher perceived lightness of the background. However, this possibility seems unsubstantial because of two reasons. First, in the control block of the fMRI experiments, illusory cylinder stimulus was shown on the screen without gratings on it. Therefore, any background lightness-dependent activity should already be subtracted from the final BOLD activity we reported. Second and more importantly, contrast type manipulation using incremental and decremental patterns enabled us to tease apart such a possibility. In decremental grating condition, contrast is increased by decreasing the luminance of grating's bars. In other words, higher contrast requires lower overall luminance. Therefore, if changes in BOLD activity are related to lightness, we would observe decrease in BOLD signal. Oppositely, we observed increase in BOLD signal related to increase in decremental contrast. Therefore, our results show that compared to lightness, the BOLD activity we observed correlates better with the changes in contrast.

It is well known that spatial frequency affects contrast perception in simple gratings [e.g., 61, 14, 54, 55, 15, 56]. For all frequencies tested we found an effect of context-dependent background lightness on perceived contrast and contrast thresholds, however there was no influence of frequency on the magnitude of the effect in the experiments conducted using the illusory checkerboard stimulus. This result does not seem to be in complete agreement with the findings of Peli and his colleagues [15], who showed that perceived contrast of high frequency gratings (e.g., 8 and 16 cycle/degree) are strongly affected by background luminance, whereas that of low-frequency gratings (e.g., 1 and 2 cycle/degree) are much less affected. The disagreement could simply be caused by differences in experimental procedures. The patterns used by Peli and his colleagues [15] were sinusoidal Gabor patches with up to 16-fold difference in spatial frequency (1 through 16 c/d), whereas here we used rectified square-wave gratings with a maximum of 4-fold difference in spatial frequency. In their study participants altered their gaze between two patterns every 1.5 seconds, whereas in our study they freely viewed the stimulus. Moreover, they used a standard grating whose spatial frequency was fixed, and the spatial frequency of their test patch varied. In our study the spatial frequencies of the standard and the match patch were equal in each trial. Therefore we did not directly compare perceived contrast across different frequencies. Instead we compared the magnitude of the effect of background lightness on perceived contrast for different spatial frequencies. Alternatively the disagreement with Peli and his colleagues' [15] results could be an indication that luminance and context-dependent lightness of the background affect perceived contrast through different mechanisms. However, in an earlier pilot study using isolated patches we failed to find an effect of frequency, which does not support such a possibility. In yet another alternative the disagreement with results might be caused by the spatial properties of the gratings we used in the experiments. We conducted additional detection threshold experiments using simultaneous brightness contrast illusion and we could see the effect of spatial frequency on detection thresholds. The size of the grating we used in this experiment was considerably larger than those superimposed on the illusory checkerboard stimulus. The effect of spatial frequency on contrast perception might be evident only when certain interactions occur with the size of the stimulus.

7.1 Conclusions

Results of this study show that perceived contrast and contrast threshold is not determined solely by the localized features of the retinal image. Context-dependent lightness, as well as actual luminance, of the background influence the perceived contrast and contrast detection and discrimination thresholds of rectified gratings. These results show that contrast perception depends neither purely on luminance nor lightness [89], instead they suggest that luminance and lightness, and contrast share common underlying mechanisms but can be assessed independently at least to some extent [27, 28, 29]. Also, neural correlates of the perceptual lightness effect on contrast perception can be observed in striate and extra-striate cortex. Therefore, it is clear that contrast is affected by visual context like many other visual features whose computation begins in the retina. Therefore, the results of this study support that although contrast is elaborately computed in retina, its computation does not end in retina. Instead, perceived contrast and contrast threshold could be determined in higher level visual areas; or alternatively in earlier areas, after receiving feedback about context-dependent lightness. Perceived contrast and contrast threshold of decremental patterns are affected differently by the context-dependent lightness and the fMRI data correlates better with the threshold data. Therefore, this study might be a neural evidence for distinct mechanisms mediating detection (modeled by threshold experiments) and identification (modeled by appearance experiments) mechanisms. However, the link between fMRI data and the threshold data is not really consistent with the recent models in the literature [e.g., 70]. These models might be insufficient to explain contrast information processing in a rich visual context. Therefore, further behavioral and neural experiments are needed in order to test the recent models especially under more naturalistic viewing conditions. New computational models are also needed.

Bibliography

[1] E. R. Kandel, J. H. Schwartz, T. M. Jessell, S. A. Siegelbaum, and A. J. Hudspeth, *Principles of neural science*, vol. 4. McGraw-hill New York, 2000.

[2] D. Purves, R. Cabeza, S. A. Huettel, K. S. LaBar, M. L. Platt, M. G. Woldorff, and E. M. Brannon, *Cognitive Neuroscience*. Sunderland: Sinauer Associates, Inc, 2008.

[3] E. B. Goldstein, *The Blackwell Handbook of Sensation and Perception*. John Wiley & Sons, 2008.

[4] S. E. Palmer, *Vision science: Photons to phenomenology*. MIT press, 1999.

[5] D. Marr, "The computation of lightness by the primate retina," *Vision research*, vol. 14, no. 12, pp. 1377–1388, 1974.

[6] L. Squire, D. Berg, F. E. Bloom, S. Du Lac, A. Ghosh, and N. C. Spitzer, *Fundamental neuroscience*. Academic Press, 2012.

[7] E. Peli, J. Yang, R. Goldstein, and A. Reeves, "Effect of luminance on suprathreshold contrast perception.," *Journal of the Optical Society of America, A*, vol. 8, no. 8, pp. 1352–1359, 1991.

[8] M. Kwon, G. E. Legge, F. Fang, A. M. Cheong, and S. He, "Adaptive changes in visual cortex following prolonged contrast reduction," *Journal of vision*, vol. 9, no. 2, pp. 20–20, 2009.

[9] J. M. Hillis and D. H. Brainard, "Distinct Mechanisms Mediate Visual Detection and Identification," *Current Biology*, vol. 17, pp. 1714–1719, 2007.

[10] D. Corney and R. B. Lotto, “What are lightness illusions and why do we see them?,” *PLoS Comput Biol*, vol. 3, no. 9, p. e180, 2007.

[11] J. Koenderink, *Visual Awareness.* Utrecht, The Netherlands: De Clootcrans Press, first ed., 2012.

[12] D. Purves, Y. Morgenstern, and W. T. Wojtach, “Perception and Reality: Why a Wholly Empirical Paradigm is Needed to Understand Vision,” *Frontiers in Systems Neuroscience*, vol. 9, pp. 1–10, 2015.

[13] A. M. Haun and E. Peli, “Perceived contrast in complex images,” *Journal of vision*, vol. 13, no. 13, pp. 3.1–21, 2013.

[14] F. L. Van Nes and M. A. Bouman, “Spatial Modulation Transfer in the Human Eye,” *Journal of the Optical Society of America*, vol. 57, no. 3, pp. 401–406, 1967.

[15] E. Peli, L. Arend, and A. T. Labianca, “Contrast perception across changes in luminance and spatial frequency.,” *Journal of the Optical Society of America, A*, vol. 13, no. 10, pp. 1953–1959, 1996.

[16] M. Kilpeläinen, L. Nurminen, and K. Donner, “Effects of mean luminance changes on human contrast perception: Contrast dependence, time-course and spatial specificity,” *PLoS ONE*, vol. 6, no. 2, pp. e17200.1–9, 2011.

[17] M. Kilpeläinen, L. Nurminen, and K. Donner, “The effect of mean luminance change and grating pedestals on contrast perception: Model simulations suggest a common, retinal, origin,” *Vision Research*, vol. 58, pp. 51–58, 2012.

[18] D. Kane and M. Bertalmiío, “The Impact of ?Crispening? upon the Perceived Contrast of Textures,” *Journal of Vision*, vol. 16, no. February, pp. 29–30, 2016.

[19] E. H. Adelson, “Lightness Perception and Lightness Illusions,” in *The New Cognitive Neurosciences* (M. Gazzaniga, ed.), ch. 24, pp. 339–351, MIT Press, 2 ed., 2000.

[20] D. Purves and R. B. Lotto, *Why We See What We Do Redux: An empirical theory of vision.* Sunderland: Sinauer Associates Sunderland, MA, 2011.

[21] B. Blakeslee and M. E. McCourt, "A unified theory of brightness contrast and assimilation incorporating oriented multiscale spatial filtering and contrast normalization," *Vision Research*, vol. 44, no. 21, pp. 2483–2503, 2004.

[22] E. Goldstein, *Sensation and perception.* Cengage Learning, 8 ed., 2009.

[23] B. L. Anderson and J. Winawer, "Image segmentation and lightness perception," *Nature*, vol. 434, no. 7029, pp. 79–83, 2005.

[24] A. H. Holway and E. G. Boring, "Determinants of apparent visual size with distance variant," *The American Journal of Psychology*, vol. 54, no. 1, pp. 21–37, 1941.

[25] R. Day, "Visual spatial illusions: A general explanation," *Science*, vol. 175, no. 4028, pp. 1335–1340, 1972.

[26] S. O. Murray, H. Boyaci, and D. Kersten, "The representation of perceived angular size in human primary visual cortex," *Nature neuroscience*, vol. 9, no. 3, pp. 429–434, 2006.

[27] J. Dai and Y. Wang, "Representation of surface luminance and contrast in primary visual cortex.," *Cerebral Cortex*, vol. 22, no. 4, pp. 776–87, 2012.

[28] W. S. Geisler, D. G. Albrecht, and A. M. Crane, "Responses of neurons in primary visual cortex to transient changes in local contrast and luminance.," *The Journal of Neuroscience*, vol. 27, no. 19, pp. 5063–5067, 2007.

[29] V. Mante, R. A. Frazor, V. Bonin, W. S. Geisler, and M. Carandini, "Independence of luminance and contrast in natural scenes and in the early visual system.," *Nature neuroscience*, vol. 8, no. 12, pp. 1690–1697, 2005.

[30] H. Boyaci, K. Doerschner, J. L. Snyder, and L. T. Maloney, "Surface color perception in three-dimensional scenes.," *Visual Neuroscience*, vol. 23, no. 3-4, pp. 311–21, 2006.

[31] F. A. A. Kingdom, “Lightness, brightness and transparency: A quarter century of new ideas, captivating demonstrations and unrelenting controversy,” *Vision Research*, vol. 51, no. 7, pp. 652–673, 2011.

[32] A. Gilchrist, “Theoretical approaches to lightness and perception,” *Perception*, vol. 44, no. 4, pp. 339–358, 2015.

[33] J. Rieger and K. R. Gegenfurtner, “Contrast sensitivity and appearance in briefly presented illusory figures.,” *Spatial vision*, vol. 12, no. 3, pp. 329–44, 1999.

[34] M. Maertens and F. Wichmann, “When luminance increment thresholds depend on apparent lightness,” *Journal of Vision*, vol. 13, no. 6, pp. 21.1–11, 2013.

[35] M. Singh and B. L. Anderson, “Toward a perceptual theory of transparency.,” *Psychological review*, vol. 109, no. 3, pp. 492–519, 2002.

[36] M. Maertens, F. a. Wichmann, and R. Shapley, “Context affects lightness at the level of surfaces,” *Journal of vision*, vol. 15, no. 1, pp. 15.1–15, 2015.

[37] E. H. Adelson, “Checker shadow illusion,” 1995.

[38] R. Shapley and R. C. Reid, “Contrast and assimilation in the perception of brightness.,” *Proceedings of the National Academy of Sciences of the United States of America*, vol. 82, no. 17, pp. 5983–6, 1985.

[39] Z. Pamir and H. Boyaci, “Context-dependent lightness affects perceived contrast,” *Vision research*, vol. 124, pp. 24–33, 2016.

[40] S. Straube and M. Fahle, “Visual detection and identification are not the same: Evidence from psychophysics and fmri,” *Brain and cognition*, vol. 75, no. 1, pp. 29–38, 2011.

[41] M. Koivisto, S. Grassini, N. Salminen-Vaparanta, and A. Revonsuo, “Different electrophysiological correlates of visual awareness for detection and identification,” *Journal of Cognitive Neuroscience*, 2017.

[42] B. R. Stephens and M. S. Banks, "The development of contrast constancy," *Journal of experimental child psychology*, vol. 40, no. 3, pp. 528–547, 1985.

[43] P. Whittle, "Increments and decrements: luminance discrimination.," *Vision research*, vol. 26, no. 10, pp. 1677–1691, 1986.

[44] C. Chubb and J. H. Nam, "Variance of high contrast textures is sensed using negative half-wave rectification," *Vision Research*, vol. 40, no. 13, pp. 1677–1694, 2000.

[45] K. A. Zaghloul, K. Boahen, and J. B. Demb, "Different circuits for ON and OFF retinal ganglion cells cause different contrast sensitivities.," *The Journal of neuroscience : the official journal of the Society for Neuroscience*, vol. 23, no. 7, pp. 2645–2654, 2003.

[46] M. E. Rudd and I. K. Zemach, "Quantitative properties of achromatic color induction: An edge integration analysis," *Vision Research*, vol. 44, no. 10, pp. 971–981, 2004.

[47] M. E. Rudd and I. K. Zemach, "The highest luminance anchoring rule in achromatic color perception: Some counterexamples and an alternative theory," *Journal of Vision*, vol. 5, no. 11, pp. 983–1003, 2005.

[48] E. Economou, S. Zdravkovic, and A. Gilchrist, "Anchoring versus spatial filtering accounts of simultaneous lightness contrast.," *Journal of vision*, vol. 7, no. 12, pp. 2.1–15, 2007.

[49] R. H. Blackwell, "Contrast thresholds of the human eye," *Journal of the Optical Society of America*, vol. 36, no. 11, pp. 624–643, 1946.

[50] A. Patel and R. Jones, "Increment and decrement visual thresholds," *Journal of the Optical Society of America*, vol. 58, no. 5, pp. 696–699, 1968.

[51] S. Rekauzke, N. Nortmann, R. Staadt, H. S. Hock, G. Schoner, and D. Jancke, "Temporal Asymmetry in Dark-Bright Processing Initiates Propagating Activity across Primary Visual Cortex," *Journal of Neuroscience*, vol. 36, no. 6, pp. 1902–1913, 2016.

[52] H. Sato, I. Motoyoshi, and T. Sato, “On-off selectivity and asymmetry in apparent contrast: An adaptation study,” *Journal of Vision*, vol. 16, no. 1, pp. 14.1–11, 2016.

[53] J. Kremkow, J. Jin, Y. Wang, and J. M. Alonso, “Principles underlying sensory map topography in primary visual cortex,” *Nature*, vol. 533, no. 7601, pp. 52–57, 2016.

[54] M. A. Georgeson and G. D. Sullivan, “Contrast constancy: deblurring in human vision by spatial frequency channels.,” *The Journal of physiology*, vol. 252, pp. 627–656, 1975.

[55] C. Chubb, G. Sperling, and J. A. Solomon, “Texture interactions determine perceived contrast.,” *Proceedings of the National Academy of Sciences*, vol. 86, no. 23, pp. 9631–9635, 1989.

[56] R. Robilotto and Q. Zaidi, “Perceived transparency of neutral density filters across dissimilar backgrounds.,” *Journal of Vision*, vol. 4, no. 3, pp. 183–195, 2004.

[57] G. W. Larson and R. Shakespeare, *Rendering with Radiance: the art and science of lighting visualization*. Morgan Kaufmann San Francisco, CA, 1998.

[58] E. Peli, “Contrast in complex images,” *Journal of the Optical Society of America, A*, vol. 7, no. 10, pp. 2032–2040, 1990.

[59] E. Peli, “Suprathreshold contrast perception across differences in mean luminance: effects of stimulus size, dichoptic presentation, and length of adaptation,” *Journal of the Optical Society of America. A, Optics, image science, and vision*, vol. 12, no. 5, pp. 817–823, 1995.

[60] F. A. A. Kingdom and N. Prins, *Psychophysics: a practical introduction*. Academic Press, 2010.

[61] F. W. Campbell and J. G. Robson, “Application of Fourier analysis to the visibility of gratings.,” *Journal of Physiology*, vol. 197, no. 3, pp. 551–566, 1968.

[62] Y. Yeshurun and M. Carrasco, "Attention improves or impairs visual performance by enhancing spatial resolution," *Nature*, vol. 396, no. 6706, pp. 72–75, 1998.

[63] M. Posner, "Orienting of attention qj exp psychol 1980; 32: 3-25."

[64] K. Herrmann, L. Montaser-Kouhsari, M. Carrasco, and D. J. Heeger, "When size matters: attention affects performance by contrast or response gain," *Nature neuroscience*, vol. 13, no. 12, pp. 1554–1559, 2010.

[65] M. Ito and C. D. Gilbert, "Attention modulates contextual influences in the primary visual cortex of alert monkeys," *Neuron*, vol. 22, no. 3, pp. 593–604, 1999.

[66] S. Kastner, P. De Weerd, R. Desimone, and L. G. Ungerleider, "Mechanisms of directed attention in the human extrastriate cortex as revealed by functional mri," *science*, vol. 282, no. 5386, pp. 108–111, 1998.

[67] L. Pessoa, S. Kastner, and L. G. Ungerleider, "Neuroimaging studies of attention: from modulation of sensory processing to top-down control," *Journal of Neuroscience*, vol. 23, no. 10, pp. 3990–3998, 2003.

[68] M. I. Sereno, A. Dale, J. Reppas, K. Kwong, *et al.*, "Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging," *Science*, vol. 268, no. 5212, p. 889, 1995.

[69] S. A. Engel, G. H. Glover, and B. A. Wandell, "Retinotopic organization in human visual cortex and the spatial precision of functional mri.," *Cerebral cortex*, vol. 7, no. 2, pp. 181–192, 1997.

[70] G. M. Boynton, J. B. Demb, G. H. Glover, and D. J. Heeger, "Neuronal basis of contrast discrimination," *Vision research*, vol. 39, no. 2, pp. 257–269, 1999.

[71] D. G. Albrecht and D. B. Hamilton, "Striate cortex of monkey and cat: contrast response function.," *Journal of neurophysiology*, vol. 48, no. 1, pp. 217–237, 1982.

[72] J. L. Gardner, P. Sun, R. A. Waggoner, K. Ueno, K. Tanaka, and K. Cheng, "Contrast adaptation and representation in human early visual cortex," *Neuron*, vol. 47, no. 4, pp. 607–620, 2005.

[73] F. Campbell and J. Kulikowski, "Orientational selectivity of the human visual system," *The Journal of physiology*, vol. 187, no. 2, p. 437, 1966.

[74] C. Bird, G. Henning, and F. Wichmann, "Contrast discrimination with sinusoidal gratings of different spatial frequency," *JOSA A*, vol. 19, no. 7, pp. 1267–1273, 2002.

[75] A. Short, "Decremental and incremental visual thresholds," *The Journal of Physiology*, vol. 185, no. 3, pp. 646–654, 1966.

[76] M. E. Rudd, "Edge integration in achromatic color perception and the lightness ? darkness asymmetry through retinex theory," *Journal of Vision*, vol. 13, no. 14, pp. 18.1–30, 2013.

[77] M. E. Rudd, "A cortical edge-integration model of object-based lightness computation that explains effects of spatial context and individual differences.," *Frontiers in Human Neuroscience*, vol. 8, p. 640, 2014.

[78] C.-I. Yeh, D. Xing, and R. M. Shapley, ""Black" responses dominate macaque primary visual cortex V1," *The Journal of Neuroscience*, vol. 29, no. 38, pp. 11753–11760, 2009.

[79] C. Olman, H. Boyaci, F. Fang, and K. Doerschner, "V1 responses to different types of luminance histogram contrast," *Journal of Vision*, vol. 8, no. 6, pp. 345–345, 2008.

[80] S. J. Komban, J.-M. Alonso, and Q. Zaidi, "Darks are processed faster than lights," *The Journal of Neuroscience*, vol. 31, no. 23, pp. 8654–8658, 2011.

[81] E. J. Chichilnisky and R. S. Kalmar, "Functional asymmetries in ON and OFF ganglion cells of primate retina.," *The Journal of Neuroscience*, vol. 22, no. 7, pp. 2737–2747, 2002.

[82] J. H. Elder, J. Victor, and S. W. Zucker, "Understanding the statistics of the natural environment and their implications for vision," *Vision Research*, vol. 120, pp. 1–4, 2016.

[83] C. P. Benton and A. Johnston, "Contrast inconstancy across changes in polarity," *Vision research*, vol. 39, no. 24, pp. 4076–4084, 1999.

[84] H. Boyaci, F. Fang, S. O. Murray, and D. Kersten, "Responses to lightness variations in early human visual cortex.," *Current Biology*, vol. 17, no. 11, pp. 989–993, 2007.

[85] S.-G. Kim, W. Richter, and K. Uğurbil, "Limitations of temporal resolution in functional mri," *Magnetic resonance in medicine*, vol. 37, no. 4, pp. 631–636, 1997.

[86] K. J. Friston, L. Harrison, and W. Penny, "Dynamic causal modelling," *Neuroimage*, vol. 19, no. 4, pp. 1273–1302, 2003.

[87] D. Takeshita, L. Smeds, and P. Ala-Laurila, "Processing of single-photon responses in the mammalian on and off retinal pathways at the sensitivity limit of vision," *Phil. Trans. R. Soc. B*, vol. 372, no. 1717, p. 20160073, 2017.

[88] C. D. Gilbert and W. Li, "Top-down influences on visual processing," *Nature Reviews Neuroscience*, vol. 14, no. 5, pp. 350–363, 2013.

[89] S. L. Guth, "On neural inhibition, contrast effects and visual sensitivity," *Vision research*, vol. 13, no. 5, pp. 937–957, 1973.

Appendix A

Contrast Detection Measurement of Incremental Gratings

This study is a pilot experiment of the detection threshold measurements conducted using the illusory checkerboard stimulus (see Chapter 3). Here, only incremental gratings at one frequency level was tested.

A.1 Methods

A.1.1 Participants

Six participants (two male) including author ZP participated in the experiment. The mean age was approximately 26.3 ranging from 22 to 31. All participants reported normal or corrected-to-normal vision, and had no history of neurological or visual disorders. Participants provided written informed consent and the experimental protocols were approved by the Human Ethics Committee of Bilkent University.

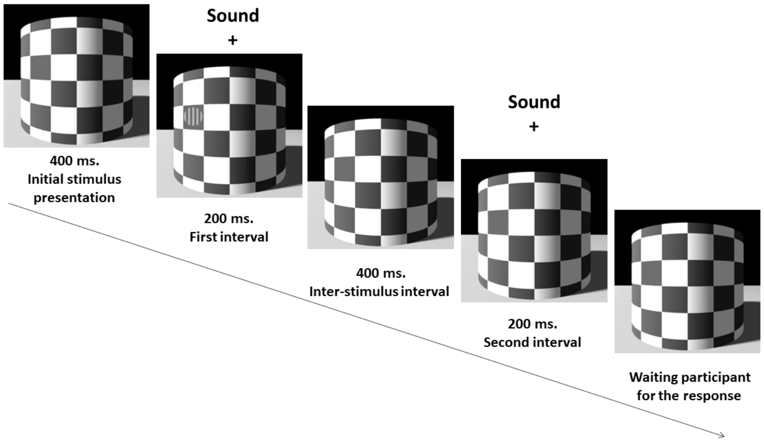

Figure A.1: Protocol for the detection threshold experiment. Gratings were superimposed on only one of the CSs, either darker or lighter, throughout a session. In each trial, grating is presented at one of the intervals selected randomly. Participants are asked to decide in which interval the grating is presented. Participants are allowed to look at target CS directly.

A.1.2 Stimuli and Design

In this experiment, the physical components of the experimental setup were the same as in the previous experiment (Section 3.1.2) unless indicated otherwise. There were slight differences in the experimental design as explained below.

In the experiment, detection thresholds were estimated using an adaptive two-interval forced-choice (2-IFC) procedure. Rectified square-wave gratings with a spatial frequency of 2 cycle/degree were superimposed on the CSs of the illusory stimulus. Gratings were superimposed on only one of the CSs, either darker or lighter, throughout a session. At the beginning of each session, participants were informed about the target CS. Each trial started with a 400-millisecond (ms) illusory stimulus presentation, followed by two intervals each presented for 200 ms. Intervals were separated by a 400-ms inter-stimulus interval (ISI) (Figure A.1), the illusory stimulus remained on the screen during the ISI. A beep-sound was presented at the beginning of each interval in order to inform participants that the interval begins. The grating was randomly presented at one of the intervals. Participants were allowed to look at target CS directly and they were asked to decide the temporal position of the grating. Two interleaved staircases with a starting point 0.002 and 0.02 contrast level (50 trials each) were applied in a single session. After each trial, contrast of the next grating was decided based on the previous responses following a 1-up 3-down adaptive staircase with 0.001 contrast steps. The contrast of the grating was decreased one step following three consecutive correct answers, and increased one step following an incorrect answer. There was no time constraint; the illusory cylinder stimulus remained on the screen until the participant made a response. Observers participated in two experimental sessions, each for one context square (left or right context square).

A.1.3 Data Analysis

Data were first analyzed with Palamedes toolbox to find the detection threshold (79% success) [60] in Octave (http://www.octave.org). Standard error of the thresholds were computed using bootstrapping. Next, using SPSS Version 19 (SPSS Inc., Chicago, IL), we applied two-tailed paired-samples Student's t-test on detection thresholds of gratings superimposed on darker and lighter CSs.

A.2 Results

Results are shown in Figure A.2. We found that the gratings superimposed on the perceptually darker context square have higher contrast detection thresholds (M = 0.015, SE = 0.002) than those superimposed on the lighter context square (M = 0.011, SE = 0.001). Two-way paired-samples t-test analysis revealed that there is a significant difference in detection thresholds (t(5)=2.6; $p < 0.05$). Thus, our results showed that gratings superimposed on equiluminant but perceptually lighter target regions were detected when contrast of grating is relatively lower than those superimposed on perceptually darker target regions.

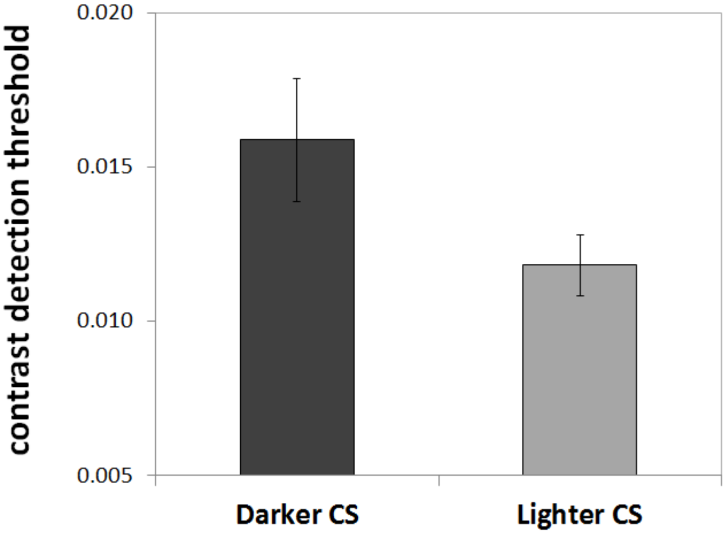

Figure A.2: Results of contrast detection experiment. Mean detection thresholds for the incremental contrast gratings superimposed on darker or lighter CSs are plotted. Detection threshold is lower for the gratings superimposed on equiluminant but perceptually lighter CS. Error bars show ±1 SEM.

A.3 Intermediate Summary and Discussion

Results of contrast detection threshold experiment showed that context-dependent lightness of the target region influences the contrast threshold of incremental gratings. Detection threshold of the incremental gratings was lower for the gratings superimposed on perceptually lighter CSs. However, in this study we did not test decremental contrast patterns. Therefore, in the main experiment (see Chapter 3) we tested both incremental and decremental contrast gratings with different frequency levels. We also made slight changes in the experimental design. Due to the configuration of the stimulus the right context square was subjectively lighter than the left one in this study. In order to eliminate possible confounds, we also used the mirror-symmetric version of the stimulus.

Appendix B

An alternative study to link behavioral and neural data

This study was first conducted as an alternative experiment to see the relationship between behavioral and neural data. In this experiment, we tested two baseline contrast levels in behavioral threshold experiments and four baseline contrasts in an FMRI study. However, we were not able to fit contrast response function to our fMRI data because of the limited number of contrast levels tested. Therefore, in order to compute the slope at the contrast levels we tested behaviorally, we conducted additional behavioral and fMRI experiments and we reported those results in Chapter 6. Here we only reported the per cent BOLD signal change across different conditions.

B.1 Discrimination threshold measurement

In this experiment, we tested detection threshold at 0% baseline contrast and discrimination threshold at 20% baseline contrast.

B.1.1 Method

B.1.1.1 Participants

Nine participants (two male) including the author ZP participated in the experiments. The mean age was approximately 27.2 ranging from 24 to 32. All participants reported normal or corrected-to-normal vision, and had no history of neurological or visual disorders. Participants provided written informed consent and the experimental protocols were approved by the Human Ethics Committee of Bilkent University.

B.1.1.2 Stimuli and Design

The stimuli were presented on a CRT monitor (HP P1230, 22 inch, 1024 X 768 resolution). To be able to present very fine-grained contrast differences, the dynamic luminance range of the monitor is increased (14-bit luminance resolution) using a digital-to-analog converter (Bits#, Cambridge Research Systems Ltd., UK). Presentation of correct luminance values was ensured by using a 14-bit gamma-corrected gray scale lookup table prepared after measurements of every four steps in a range that is necessary for generation of our stimuli with a colorimeter (SpectroCAL,Cambridge Research Systems Ltd., UK). Values of other steps were defined by interpolation. Participants were seated 75 cm from the monitor, and their heads were stabilized using a chin rest. Participants' responses were collected via a standard computer keyboard.

The illusory checkerboard stimulus subtended 20 by 20 degrees of visual angle. Approximate size of the context squares was 2.65 by 2.65 degrees of visual angle. Luminance of the context square was 8.17 cd/m^2. Rectified square-wave gratings weighted by two-dimensional isotropic Gaussian envelopes were superimposed on the context squares of the illusory stimulus. Incremental and decremental gratings with frequency of 2 cycles/degree were tested. Contrast of the gratings was defined by Weber Contrast. In the experiment, contrast detection and discrimination thresholds were measured at two baseline contrasts (0% and 20% contrast levels), using an adaptive two-interval forced-choice (2-IFC) procedure. Two baseline contrasts were tested in different sessions. At the beginning of each trial, either original checkerboard stimulus or the mirror-symmetric version of it presented randomly. Gratings were superimposed on only the right CS, which might be either darker or lighter depending on the trial, throughout a session. Each trial started with a 3000 ms illusory stimulus presentation, followed by two intervals each presented for 500 ms. Intervals were separated by a 500-ms inter-stimulus interval (ISI), the illusory stimulus remained on the screen during the ISI. Dark and light CSs were tested within the same session. Two interleaved staircases were applied for each CS independently (4 staircases in total, each containing 60 trials, 240 trials in total) in a single session. After each trial, contrast of the next test grating was decided based on the previous responses following a 1-up 3-down adaptive staircase with 0.003 contrast steps for 0% and 0.005 contrast steps for 20% baseline contrast. Observers participated in four experimental sessions (2 contrast type (incremental or decremental) X 2 baseline contrast levels (0% or 20%)).

B.1.1.3 Data analysis

Data were first analyzed as it is explained in Section A.1.3. For decremental contrasts, before computing the threshold, we first converted the levels to positive values. Raw data were converted to discrimination threshold by subtracting the threshold from baseline contrast level.

We conducted repeated measures ANOVA with three factors (contrast type, CS, contrast level) and thresholds for different CSs were compared using a two-tailed paired-samples Student's t-test in SPSS.

B.1.2 Results

Results are shown in Figure B.1. Similarly to previous experiments, main effect of CS was statistically significant (F(1,8) = 19.27, $p < 0.01$). Mean discrimination threshold for the gratings superimposed on darker CS (M = 0.028, SEM = 0.001) was higher than that on the lighter CS (M = 0.024, SEM = 0.002). Also, main effect of contrast (F(1,8) = 60.56, $p < 0.001$) was statistically significant. Mean discrimination threshold for the gratings with 20% baseline contrast (M = 0.039, SEM = 0.003) was higher than that with the 0% baseline contrast (M = 0.013, SEM = 0.001) as expected considering a typical TvC curve. Also, similarly to previous results, main effect of contrast type was not significant (F(1,8) = 3.78, $p > 0.05$).

Detection threshold at 0% baseline contrast was significantly higher when gratings were superimposed on perceptually darker CSs than that on lighter CSs both for incremental (for lighter CS: M = 0.0109, SEM = 0.0006; for darker CS: M = 0.0143, SEM = 0.001; t(8) = 5.36, $p < 0.01$) and decremental gratings (for lighter CS: M = 0.0124, SEM = 0.0005; for darker CS: M = 0.0152, SEM = 0.007; t(8) = 8.68, $p < 0.01$). Results were similar for discrimination thresholds at 20% baseline contrast. For the incremental gratings, there was a significant difference in discrimination thresholds of gratings superimposed either on lighter or darker CS (for lighter CS: M = 0.038, SEM = 0.003; for darker CS: M = 0.045, SEM = 0.002; t(8) =2.44, $p < 0.05$). The same trend was observed for decremental gratings, and the difference was close to significance (for lighter CS: M = 0.034, SEM = 0.003; for darker CS: M = 0.038, SEM = 0.004; t(8) = 1.926, $p = 0.09$).

B.1.3 Intermediate Summary and Discussion

Results of the present experiment was consistent with the previous results. For the detection threshold, a lower contrast is required in order to detect the presence of a grating when it is superimposed on perceptually lighter CS compared to the condition that gratings were superimposed on perceptually darker CS. Also, as

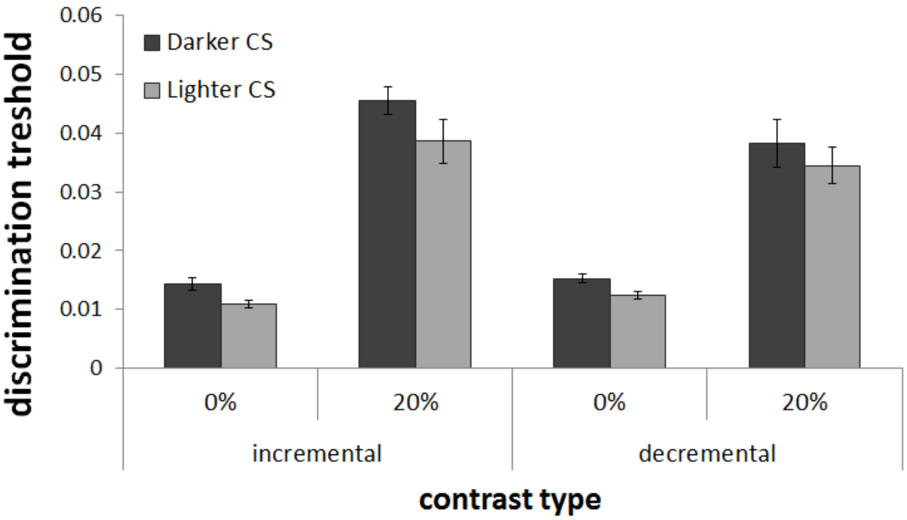

Figure B.1: Discrimination Thresholds for the incremental and decremental gratings superimposed on either darker or lighter CSs. Discrimination threshold is higher when gratings are superimposed on darker CS. Error bars show ±1 SEM.

we predicted, the same trend was observed for decremental gratings. Here compared to the previous experiment, context-dependent lightness effect on contrast threshold was stronger. After ensuring that context-dependent lightness affects contrast discrimination thresholds, we conducted fMRI experiments.

B.2 fMRI of Contrast Discrimination Measurement

In order to compute the slope at the contrast levels we tested behaviorally, we collected data from four contrast levels (0% and 5% for the 0% baseline contrast tested behaviorally, and 20% and 30% for the 20% baseline contrast tested behaviorally) in the fMRI study.

B.2.1 Method

B.2.1.1 Participants

Six participants (three male) including author ZP participated in the experiment. Five of them were also participated behavioral discrimination threshold measurement experiments. Mean age was 26 ranging from 23 to 29. Participants provided written informed consent and the experimental protocols were approved by the Human Ethics Committee of Bilkent University.

B.2.1.2 Stimuli and Design

B.2.1.2.1 Behavioral Experiment in the Scanner For this experiment, we replicated our previous adjustment experiments in the scanner. Differently from those experiments, the standard grating was placed on one of the CSs and the match grating was placed on the other CS. Although monitor properties were the same with the previous fMRI experiments, the viewing distance was changed to 162 cm due to some technical problems. The approximate size of the grating was 1.68 degree.

B.2.1.2.1.1 Data Analysis Analyses were performed on averaged perceived contrast scores. In order to test whether perceived contrasts of gratings superimposed on either darker or lighter CSs are significantly different, we conducted two-tailed paired-samples Student's t-test in SPSS. For decremental contrasts, before computing the mean perceived contrast, we first converted the levels to positive values.

B.2.1.2.2 fMRI Experiment The fMRI experiment included an anatomical scan, a functional localization scan, and eight experimental scans. The illusory checkerboard stimulus was used in the experiments. Photometrically identical gratings were superimposed on both context squares simultaneously. 0% baseline contrast condition and 20% baseline contrast condition were tested in different runs. In the first 24 seconds subjects viewed only the illusory stimulus without gratings. In a block design, subjects viewed five 12-second alternating blocks of three conditions. In the first condition, gratings with baseline contrast (either 0% or 20%), and in the second condition, gratings with slightly higher contrast than baseline contrast (either 5% or 30%) were presented (experimental blocks). Experimental blocks were separated by control blocks that gratings were absent on a checkerboard stimulus. In all blocks, subjects viewed the fixation mark.

Gratings were flickering at 4 Hz to avoid adaptation of neurons. One of the flickering gratings is frozen for 500 milliseconds randomly in every 2000-4000 milliseconds. Participants were asked to fixate the fixation mark, and they are required to detect the grating that has been frozen. Eight fMRI scans were applied; two for different baseline contrast levels and two for different contrast types. Each condition was repeated two times in one of which mirror-symmetric version of the stimulus was presented. Also, an additional functional region of interest (ROI) localization scan was applied in the main fMRI experiment.

B.2.1.2.2.1 Region of Interest (ROI) localization Both anatomical (Figure 5.3) and functional ROIs (Figure 5.4) were defined as it is explained in Section 5.2.1.3. Differently here, two contrast levels, either 5% or 20%, were presented in alternating experimental blocks which were separated by 12 seconds control blocks.This cycle was repeated for five times in a scan. Also, similar with experimental scans in this experiment, in this scan, one of the flickering gratings is frozen for 500 milliseconds randomly in every 2000-4000 milliseconds. Participants were asked to fixate the fixation mark, and they are required to detect the grating that has been frozen.

B.2.1.2.2.2 MRI data acquisition Scanning protocols were as explained in Section 5.2.1.4.

B.2.1.2.2.3 fMRI data processing and analyses MRI data were preprocessed and ROIs were defined as it is explained in 5.2.1.5. For each experimental scan, the time course and event-related average of fMRI signals from defined ROIs was extracted. For each fMRI scan, the time course of BOLD responses was extracted by averaging the data across all the voxels within the pre-defined ROI, and then normalized by the mean BOLD signal across the scan. Also, mean BOLD signal of three time points before the stimulus onset were normalized to zero for each condition. An event-related averaging were then performed by averaging time points of experimental block from third to fifth (between 6 and 12s) starting at the stimulus onset. We first fitted the CRFs to the data using the protocols explained in Section 6.2.2.1.5. However, those fits were not very successful because of the limited number of contrast levels we tested. Therefore, results were not reported here. Additionally, a repeated-measures ANOVA was conducted in order to test three factors: contrast type (two levels: incremental, decremental), contrast level (two levels: 0%, 20%), and CS (two levels: darker, lighter). Additionally, a two-tailed paired-samples Student's t-test was applied in SPSS to the data corresponding to darker and lighter CSs for each condition separately.

B.2.2 Results

B.2.2.1 Behavioral Experiment in the Scanner

Behavioral results in the scanner are shown in Figure B.2. For the incremental grating condition, perceived contrast of gratings superimposed on lighter CSs was higher than those superimposed on darker CS (t(5)= 3.59, $p < 0.05$). For the decremental grating condition, the difference was not significant (t(5)= 0.22, $p > 0.05$). In this experiment, consistent with our previous adjustment experiments, we found that perceived contrast increased with context-dependent lightness of the background for incremental gratings, but not for decremental gratings.

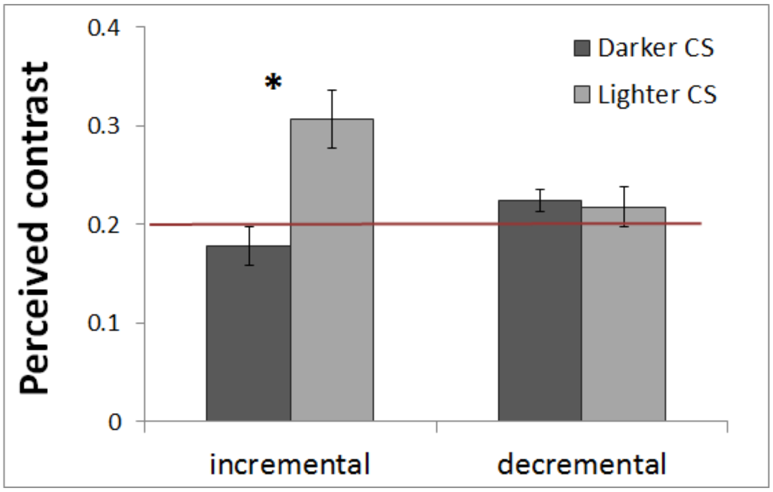

Figure B.2: Mean settings in the perceived contrast experiment in the scanner. Red horizontal line corresponds to the actual contrast. * $p < 0.05$. Error bars show ±1 SEM.

B.2.2.2 fMRI Experiment

We could define the functional ROIs only in V1 and only for three participants. Therefore, further analyses are conducted using data from three participants. Event-related averages in pre-defined functional ROI in V1 for incremental and decremental contrast stimuli are plotted in Figure B.3. Below, detailed results are reported.

Analyses showed that the only significant main effect was CS (F(1,2) = 19.5, $p < 0.05$). Bold signal change was higher when grating were superimposed on perceptually lighter CS (M = 0.42, SEM = 0.12) than those superimposed on darker CS (M = 0.15, SEM = 0.12). Despite the limited number of data, two-tailed paired-samples Student's t-test results showed that for the most of the conditions tested (six out of eight, see Figure B.3) there was a significant difference or a trend in thresholds for the gratings superimposed either darker or lighter CSs. Results showed that for both contrast types, BOLD activity in V1 tended to increase when identical gratings were superimposed on perceptually lighter CS.

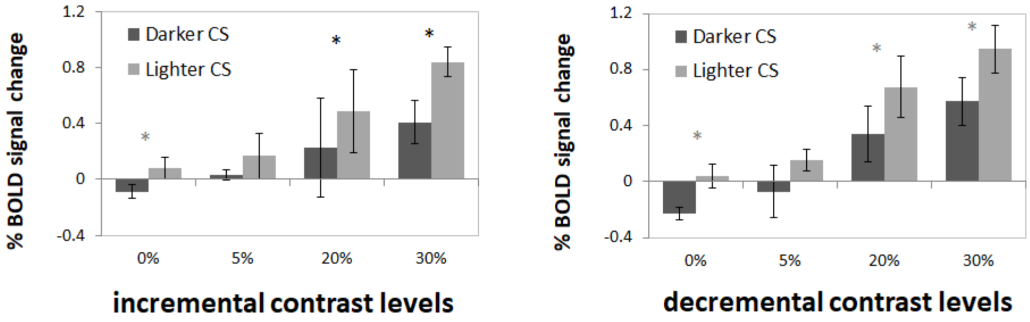

Figure B.3: Results of fMRI experiments. For each condition, trial-onset-locked event-related averages in V1 within pre-defined functional ROIs were calculated for three subjects. Data at 3rd, 4th, and 5th TR points were averaged for comparison between conditions. $*p < 0.05$ Lighter $*\ p < 0.1$. Error bars show ±1 SEM.

B.2.3 Intermediate Summary and Discussion

Results of the present fMRI experiment is consistent with our previous fMRI experiments. BOLD response is higher for the gratings superimposed on lighter CS than those superimposed on darker CS. Also, as the contrast increases, BOLD response increases both for incremental and decremental contrast patterns. However, in this study we had a difficulty of defining functional ROIs. In our fMRI experiments, we always defined functional ROI in a different scan within the main experimental session. However, we used different fixation tasks in the experiments. In the previous study, participants' task were detecting changes in fixation mark's color by pressing response button. In the present study, one of the flickering gratings superimposed on CSs is frozen. Participants were asked to fixate the fixation mark, and they are required to detect the grating that has been frozen. This new task has yielded an extensive negative BOLD within the occipital cortex that disable us to define active voxels within the functional ROI scan. Also, because of the limited number of contrast levels we tested in the fMRI experiments we could not compute the slopes effectively. Therefore, additional experiments were conducted and reported in the main text in Chapter 6.