Vision Research 116 (2015) 80–91

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

The dynamics of cross-orientation masking at monocular and interocular sites

Yeon Jin Kim [*], Kathy T. Mullen

McGill Vision Research, Department of Ophthalmology, McGill University, Montreal, Quebec H3G 1A4, Canada

A R T I C L E   I N F O

Article history:
Received 26 May 2015
Received in revised form 9 September 2015
Accepted 21 September 2015

Keywords:
Color vision
Temporal properties
Psychophysics
Dichoptic
Isoluminance

A B S T R A C T

We investigated the temporal properties of monocular and dichoptic cross-orientation masking (XOM) mediating suppressive or facilitatory cross-channel interactions between the neural detectors for the test and orthogonal mask stimuli. We measured the evolution of masking as a function of the duration of the test and mask stimuli to determine its time constant, and determined its dependence on stimulus onset asynchrony (SOA), for three contrast combinations: color-only (red–green color test and mask), luminance-only (luminance test and mask) and color-luminance (color test and luminance mask). Results show that the temporal properties of monocular and dichoptic masking differ markedly from each other and across contrast type. For the color-only condition, the dichoptic suppressive interaction is significantly longer than for the monocular one and both are largely independent of SOA. For the luminance-only condition, the suppressive interactions in both presentations are faster than for color, have similar time constants, but have different dependencies on SOA. For the color-luminance condition under the monocular conditions, cross-orientation facilitation (XOF) occurs with the luminance mask speeding up the processing of the color test with greatest XOF when the luminance mask precedes the color test by around 22 ms. No significant effects are observed for the dichoptic condition. Effects are invariant across spatial frequency. These strongly differential dynamic effects suggest that there is separate encoding of color contrast, luminance contrast, and their combination at the relatively early within-eye stage of processing, which is distinct from the dichoptic site.

1. Introduction

Cross-orientation masking (XOM) is a widely-known psychophysical phenomenon, in which the detection of a test stimulus, such as a grating, is masked by a superimposed stimulus with an orthogonal orientation. This phenomenon, also called overlay masking, is one of the most prevalent forms of suppression in the visual system, and has been extensively investigated in luminance vision (Cass, Stuit, Bex, & Alais, 2009; Foley, 1994; Holmes & Meese, 2004; Meese & Hess, 2004; Meese & Holmes, 2007; Meier & Carandini, 2002; Petrov, Carandini, & McKee, 2005), but less so in color vision (Kim, Gheiratmand, & Mullen, 2013; Medina & Mullen, 2009; Mullen, Kim, & Gheiratmand, 2014). XOM is widely thought to be the result of cross-channel interactions, based on mutual suppression between the neural detectors for the test and for the orthogonal mask stimuli, tuned to different orientations. This mutual suppression in neural activity is referred to as contrast gain control, and has been well characterized by several models of contrast normalization, in which the activity of a neural detector at an early visual stage (V1) is divided by the pooled activities of a number of neural detectors forming a contrast gain control pool, in a so-called “divisive normalization” process (Bonds, 1989; Carandini & Heeger, 2012; Carandini, Heeger, & Movshon, 1997; Foley, 1994; Geisler & Albrecht, 1992; Heeger, 1992).

Suppression underlying psychophysical XOM is thought to occur in at least two different ocular sites. One is within-eye suppression that occurs within a monocular channel, and the other is interocular suppression that occurs between monocular channels. These two types of suppression have been well accounted for by contrast normalization models of cross-orientation masking in luminance contrast (Baker, Meese, & Summers, 2007; Kim et al., 2013; Meese & Baker, 2009), color contrast (Kim et al., 2013), and color and luminance contrast in combination (Mullen et al., 2014). Evidence suggests that for luminance vision these two types of suppression engage mechanisms that are distinct in terms of their spatio-temporal properties (Meese & Baker, 2009), their response to stimulus duration and their response to adaptation

---

[*] Corresponding author at: McGill Vision Research, Department of Ophthalmology, L11.513, 1650 Ave Cedar, Montreal, Quebec H3G 1A4, Canada.

E-mail address: yeon.jin.kim@gmx.us (Y.J. Kim).

http://dx.doi.org/10.1016/j.visres.2015.09.008
0042-6989/

(Baker et al., 2007), and in terms of orientation tuning (Baker & Meese, 2007). Likewise for color vision, within-eye and interocular suppression appear distinct in several ways. For within-eye conditions, chromatic cross-orientation suppression (XOS) is stronger than the equivalent achromatic effect and is selective for color contrast, whereas under dichoptic conditions the two effects have a similar magnitude and suppression is not chromatically selective, with both achromatic and chromatic contrast suppressing chromatic stimuli (Kim et al., 2013; Mullen et al., 2014).

Studying the dynamics of XOM will help our understanding of the underlying mechanisms involved in these two types of suppression. Smith, Bair, and Movshon (2006) have investigated the temporal dynamics of XOS in macaque V1 neurons (using achromatic contrast) searching for indications of the source of within-eye suppression. They found that the onset of XOS was fast and appeared to act on the neuron even before the response onset for the preferred grating (Smith et al., 2006). They suggested that the underlying mechanism must be a rapid direct feed-forward intracortical inhibition forming divisive normalization signals in V1 cortex.

Psychophysical studies have also investigated the temporal properties of monocular and dichoptic masking. Baker et al. (2007) compared the evolution of monocular and dichoptic XOM in luminance contrast as a function of the stimulus duration of the test and mask stimuli and found that monocular masking is markedly different from dichoptic masking, with monocular masking being more dependent on stimulus duration than dichoptic masking (Baker et al., 2007). Interestingly, a recent clinical approach by Zhou et al. (2014) examined the time course of dichoptic masking using broadband noise masks in normal vision and suppression in amblyopia to understand the relationship between them. They found that interocular suppression derived from dichoptic stimuli and suppression in amblyopia have similar temporal properties in that both are strongest at short durations and decreased to approach a plateau as stimulus duration increased. Other studies have investigated the temporal properties of masking by varying the temporal interval between test and mask stimuli under other conditions (Brietmeyer, 1984; Brietmeyer & Ogmen, 2000; Essock, Haun, & Kim, 2009; Georgeson & Georgeson, 1987; Macknik & Livingstone, 1998; Saarela & Herzog, 2008). The agreement across studies is that masking occurs when the transient responses to the target are inhibited by the transient onset or offset responses to the mask stimuli, indicating a critical role of the temporal interactions between specific parts of the responses elicited by each of the test and the mask stimulus (i.e., Macknik & Livingstone, 1998).

Here we use XOM to investigate the temporal properties of monocular and dichoptic contrast normalization, mediating either suppressive or facilitatory cross-channel interactions for color-only (color test and mask), luminance-only (luminance test and mask) and color-luminance (color test and luminance mask) conditions. We first investigate the integration time for the color and luminance test stimuli presented alone. We then explore the time course of XOM by measuring the masking effect as a function of the duration of the test and mask stimuli and determining its time constant (Experiment 1). This reveals how the mask influences the time course of the detection of the test stimulus in monocular as compared to dichoptic conditions under our three contrast types at two spatial frequencies (0.375 and 1 cpd). In a second experiment, we explore the temporal resolution of the XOM by measuring masking as a function of stimulus onset asynchrony (SOA) between the test and mask stimuli in two viewing conditions (at 0.375 cpd) across the three contrast types, and determining its temporal bandwidth (Experiment 2).

Results show that the temporal properties of monocular and dichoptic cross-channel interactions are markedly different from each other, and differ profoundly across the three contrast types. For color contrast (color-only condition), the suppressive interactions under dichoptic viewing are significantly more prolonged than those for monocular viewing, and both types of suppression are prolonged across a wide range of SOAs. For achromatic contrast (luminance-only condition), the suppressive interactions under both viewing conditions are faster than in color vision, and show differential tuning for SOA. Interestingly, for a color test in the presence of an achromatic mask (color-luminance condition), we observe a different set of interactions particularly for the monocular condition, with strong *facilitation*. The luminance mask speeds up processing of the color test, and the greatest facilitation occurs when the luminance mask precedes the color test by around 22 ms (forward facilitation). For dichoptic viewing, there is no significant temporal effect of the luminance mask on the color test. These results suggest that there is differential dynamic encoding of color contrast, luminance contrast and their combination at a relatively early monocular site, which is independent of the interocular site.

2. Methods

2.1. Apparatus

Stimuli were displayed on a Sony Trinitron (GDM 500DIS) monitor (Sony Corporation, Tokyo, Japan) at 120 Hz frame rate and 1024 × 768 spatial resolution. A ViSaGe video-graphics card (Cambridge Research Systems, Kent, UK) was used to provide 14-bit contrast resolution using CRS Toolbox for MATLAB (MathWorks version 2008b). The monitor was gamma corrected and color calibrated as described previously (Kim et al., 2013). The background was achromatic with a mean luminance of 51 cd/m^2 at the screen center. All stimuli were viewed through a mirror stereoscope in a dimly lit room with a viewing distance of 58 cm.

2.2. Observers

Three subjects participated in this study, the one author (YJK) and two naïve subjects (AR and IO). All had normal or corrected-to-normal visual acuity and normal color vision. The experiments were performed in accordance with the Declaration of Helsinki and approved by the institutional ethics committee of McGill University Health Center. Each subject signed an informed consent form.

2.3. Color space

Stimuli were represented in a 3-dimensional cone-contrast space (Cole, Hine, & McIlhagga, 1993; Sankeralli & Mullen, 1996) in which each axis is defined by the contrast of the stimulus to each cone type. The calculation of this space has been described previously (Kim et al., 2013). Stimulus contrast is defined as the vector length in cone contrast units (C_C):

$$C_C = \sqrt{(L_C)^2 + (M_C)^2 + (S_C)^2} \tag{1}$$

where L_c, M_c, and S_c represent the L, M, and S Weber cone-contrast fractions in relation to the L, M, and S cone values of the achromatic background. The isoluminance point for the red–green mechanism was estimated by a minimum motion task (Cavanagh, Tyler, & Favreau, 1984) for each observer and for each spatial frequency.

2.4. Stimuli

Test stimuli were chromatic (red/green) or achromatic horizontal Gabor patterns. Chromatic stimuli were isoluminant and