Very few exclusive percepts for contrast-modulated stimuli during binocular rivalry

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ABSTRACT

Binocular rivalry properties for contrast-modulated (CM) gratings were examined to gain insight into their locus of processing. Two orthogonally orientated gratings were presented, one to each eye. Perceptual change rates, proportions of exclusivity and mixed percepts, and mean durations were calculated. Stimuli were noiseless luminance-defined (L), luminance-modulated noise (LM) and contrast-modulated noise (CM) gratings with sizes of 1, 2 and 4 deg and spatial frequencies of 4, 2 and 1 c/deg, respectively. For the LM and CM gratings, binary noise was fully correlated between eyes. Maximum producible modulations were used (1.0 for CM, 0.78 for LM and 0.98 for L stimuli). In a control experiment, contrasts of LM gratings were reduced until the multiples over detection threshold were similar to those of CM stimuli. Trial durations of 120 s were analyzed. Exclusive visibility decreased with increasing stimulus size regardless of the stimulus type. Even with visibilities at similar multiples above detection threshold, significantly lower proportions of exclusive percepts and perceptual changes were found for CM, compared to LM gratings. The results obtained with dichoptically presented orthogonal CM gratings are significantly different from those obtained for orthogonal gratings presented to one eye. CM stimuli therefore do engage in binocular rivalry but with different characteristics to those found for LM stimuli. These results suggest that CM stimuli are processed by a mechanism that promotes binocular combination rather than rivalry, and therefore may involve cells in a higher visual area than those that initially process LM information.

1. Introduction

Incompatible stimuli presented dichoptically can provoke competition between visual percepts, known as binocular rivalry (e.g. Breese, 1899, 1909; Levelt, 1965; Wheatstone, 1838). As a result of conflict during binocular rivalry, for a few seconds just one image will be perceived exclusively, whilst the other is suppressed. The dominance phases alternate between the two eyes over time. Different states of mixed percepts can also occur and can be categorized into piecemeal, when the perceived image is made up of portions of each stimulus (e.g. Blake, 1989), superimposition in which both stimuli are perceived in their entirety, overlapping each other (e.g. Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006; and see also Liu, Tyler, & Schor, 1992), and transparency superimposition, where rival stimuli with very different spatial frequencies are seen at the same time, overlapping each other, but with one appearing in front of the other (Yang, Rose, & Blake, 1992).

It has been suggested that competition between mainly monocular neurons is involved in the processing of exclusively visible percepts during traditional binocular rivalry (see review Tong, Meng, & Blake, 2006). In contrast, mixed states might represent the integration of two images at areas receiving predominantly binocular input along the visual pathway (Brascamp et al., 2006; Klink, Brascamp, Blake, & van Wezel, 2010; see also Liu et al., 1992).

Both early and later stages of the visual pathway are involved in binocular rivalry and sometimes stimulus rivalry overcomes binocular rivalry. For example, two rivalrous images shown to the two eyes, but with each containing parts of two stimuli, generate visual exclusivity of whole stimuli as a result of interocular grouping (Diaz-Caneja's, 1928 translated by Alais et al. (2000); Kovács, Papathomas, Yang, & Feher, 1996), suggesting that binocular rivalry can lead to competition between percepts, rather than between eyes. Results of neuro-imaging studies also support the engagement of both low (Lee & Blake, 2002; Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001; Wunderlich, Schneider, & Kastner, 2005) and high visual areas (Tong, Nakayama, Vaughan, & Kanwisher, 1998; Buckthought, Jessula, &

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Mendola, 2011), as do results from a study using single-unit recordings from monkey (Leopold & Logothetis, 1996). Visual attention, a higher cortical process, also contributes to binocular rivalry (for review, see Paffen & Alais, 2011) and eye movements might influence alternation of perception as saccades occur with high probability, just before an alternation during rivalry (Van Dam & van Ee, 2006b). Nonetheless, traditional psychophysical studies have demonstrated that characteristics of binocular rivalry strongly depend on stimulus properties, such as contrast (Bossink, Stalmeier, & De Weert, 1993; Levelt, 1965) and size (Blake, O'Shea, & Mueller, 1992; Breese, 1909; O'Shea, Sims, & Govan, 1997), which are first encoded at a low-level of the visual system.

Previous studies have predominantly used stimuli that contained elements differentiated from their background by luminance differences, called first-order or luminance-defined (L) stimuli. The visual system is also capable of distinguishing between visual stimuli that differ from their background by changes in contrast, called second-order, or contrast-modulated (CM) stimuli. CM stimuli can be constructed by modulating visual noise. To examine the effects of noise per se on stimulus processing, the same noise characteristics used to create CM stimuli, can be added to luminance-defined stimuli, to create luminance-modulated (LM) stimuli. Both L and LM stimuli are in fact "lumi nance-defined", but in this context, the luminance-defined (L) stimuli modulate the noiseless background luminance, whereas luminance-modulated (LM) stimuli modulate the background that contains noise. The ability to locate and identify second-order information can be explained by a "filter-rectify-filter" model (e.g. Landy & Graham, 2004; Mareschal & Baker, 1999; and see also Zhou & Baker, 1993). In this model, a linear spatiotemporal filter gives an orientation- and spatial frequency-selective response to luminance. Then, the rectified output of the first filter is passed to a second linear filter that responds selectively to variations in the outputs of the first-order filters and represents this variation across regions of an image.

Strong psychophysical evidence for separate mechanisms for the monocular processing of first- and second-order information was presented by Schofield and Georgeson (1999). The participant had to detect LM or CM test gratings superimposed on weak LM and CM grating backgrounds. The results showed that LM background gratings facilitate the detection of LM test gratings, and CM background gratings also facilitate the detection of CM test gratings. However, only very slight or no facilitation was found for the detection of LM gratings on a CM background, or vice versa.

Psychophysical support for differently sized processing mechanisms of LM and CM stimuli comes from a study by Sukumar and Waugh (2007) who made spatial summation estimates at the fovea and at various eccentricities (up to 10 deg) for blob detection. Participants had to detect dynamic binary noise LM and CM Gaussian blobs of various sizes. Spatial summation areas for the processing of CM blobs were bigger than those of LM blobs at all eccentricities. The authors speculated that this finding may be explained by a V2 site of second-order processing.

Human cortical electric activity in the brain evoked with LM and CM dynamic binary noise gratings (Calvert, Manahilov, Simpson, & Parker, 2005) has also been investigated. Visual evoked potential measurements were carried out whilst the participant gave responses to a psychophysical detection task for L, LM, and CM gratings. A significantly longer latency for CM gratings compared to LM gratings was found in the occipital area. Being in line with the "filter-rectify-filter" model, the authors speculated that the longer latency for second-order stimuli was due to additional processing in higher cortical areas for CM, than for LM stimuli. Larsson and collaborators presented first- and second-order texture defined grating stimuli and measured the metabolic activity in a wide range of lower and higher cortical visual areas

(Larsson, Landy, & Heeger, 2006). Both LM and CM stimuli generate activity in various areas (V1, V2, V3, V3 A/B, and in the visual areas anterior to dorsal V3 called L01, hV4, and V01). Whilst for LM stimuli the activity in extrastriate areas was the same as in V1, CM stimuli generated larger activity in areas beyond V1 (e.g. V01).

The involvement of areas receiving predominantly binocular input, i.e. beyond the entry level of V1, in the visual processing of CM stimuli was also suggested by Wong, Levi, and McGraw (2001). Detection thresholds for LM and CM stimuli were measured monocularly in individuals with amblyopia (a disorder of binocularity), and for the dominant eyes of healthy individuals. In almost all amblyopic, and in some preferred eyes of amblyopes, a relatively greater detection loss for CM, compared to LM stimuli was found. Visual sensitivity loss for amblyopic and preferred eyes in amblyopes to second-order information in particular, led Wong and collaborators to suggest that neurons involved are substantially more binocular, than those that process first-order information. In a study of inter-ocular blur suppression of first- and second-order stimuli by Chima, Formankiewicz, and Waugh (2015), binocularity of the visual system was disturbed by blurring one eye. Use of CM rather than LM stimuli resulted in deeper measures of inter-ocular suppression. This suggests that CM envelope extraction and combination across the two eyes occurs at a later stage of visual processing, than where binocular combination of the LM stimuli would first take place.

The evidence presented above suggests that the initial site for processing of CM stimuli lies further along the visual pathway than for LM stimuli. However, we know very little about the perception of CM stimuli under binocular rivalry conditions. An investigation of CM perception during binocular rivalry will help to enhance the understanding of the processing mechanisms of CM stimuli in the early visual cortex. In addition, the different processing sites that have been proposed for CM and LM stimuli might give rise to different characteristics of binocular rivalry for the two types of stimuli.

2. Methods

2.1. Observers

Six male and five female participants with an average age of 25.8 (± 5.4 standard deviation) years completed the study. One participant was excluded because of ongoing lack of concentration during the experimental task. Four of the ten remaining participants were experienced observers in binocular rivalry experiments (including one of the authors, J.S.) whilst the other six were inexperienced psychophysical observers. All observers except author J.S. were naïve to the purpose of the study. All observers had normal or corrected-to-normal vision with visual acuity of at least 6/6 and normal binocular vision as indicated by random-dot-stereopsis of at least 60 arcsec when measured with the Dutch Organization for Applied Scientific Research (TNO) stereo test (Lameris Ootech, Ede, Netherlands).

2.2. Stimuli

Three different stimulus types were used for the experiment (see Fig. 1):

The three stimulus types, illustrated in Fig. 1 can be mathematically described by the following equations (Calvert et al., 2005; Schofield et al., 1999).

Sinusoidal luminance (L) grating:

$$l_0(x, y) = l_0[1 + l\sin(2\pi x f_x)]$$

$l_0(x, y)$ is the luminance at position (x, y), l_0 is the mean luminance, l is the luminance modulation and f_x is the spatial frequency.