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PSYCHOPHYSICAL EVIDENCE FOR TWO ROUTES TO SUPPRESSION BEFORE BINOCULAR SUMMATION OF SIGNALS IN HUMAN VISION

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Abstract—Visual mechanisms in primary visual cortex are suppressed by the superposition of gratings perpendicular to their preferred orientations. A clear picture of this process is needed to (i) inform functional architecture of image-processing models, (ii) identify the pathways available to support binocular rivalry, and (iii) generally advance our understanding of early vision. Here we use monoptic sine-wave gratings and cross-orientation masking (XOM) to reveal two cross-oriented suppressive pathways in humans, both of which occur before full binocular summation of signals. One is a within-eye (ipsiocular) pathway that is spatially broadband, immune to contrast adaptation and has a suppressive weight that tends to decrease with stimulus duration. The other pathway operates between the eyes (interocular), is spatially tuned, desensitizes with contrast adaptation and has a suppressive weight that increases with stimulus duration. When cross-oriented masks are presented to both eyes, masking is enhanced or diminished for conditions in which either ipsiocular or interocular pathways dominate masking, respectively. We propose that ipsiocular suppression precedes the influence of interocular suppression and tentatively associate the two effects with the lateral geniculate nucleus (or retina) and the visual cortex respectively. The interocular route is a good candidate for the initial pathway involved in binocular rivalry and predicts that interocular cross-orientation suppression should be found in cortical cells with predominantly ipsiocular drive.

Key words: human vision, psychophysics, cross-orientation inhibition, contrast gain control, masking, binocular rivalry.

Masking is the psychophysical phenomenon whereby the addition of a ‘mask’ stimulus to a target image causes information in the target to be lost to the observer. There are probably several different processes involved in the various masking phenomena in the literature (Harmon and Julesz, 1973; Legge and Foley, 1980; Morrone et al., 1983; Born and Tootell, 1991; Foley, 1994; Olzak and Thomas, 1999; Macknik and Martinez-Conde, 2004; Meese and Holmes, 2007), but one which is thought to underlie several of them is suppression. Of particular interest here is the variant known as cross-orientation suppression (XOS): a cell’s response to a stimulus at its preferred orientation is reduced by the superposition of a mask stimulus at another orientation (Morrone et al., 1982; Bonds, 1989). Early work supposed that XOS is caused by intra-cortical inhibition (Morrone et al., 1987; Heeger, 1992), but recent studies of cat physiology have challenged this view. For example, mask stimuli that drift or flicker too quickly to excite most cortical cells will nevertheless produce XOS, implying pre-cortical involvement (Freeman et al., 2002; Sengpiel and Vorobyov, 2005). Possible origins include suppressive interactions in the lateral geniculate nucleus (LGN) (Levick et al., 1972; Bonin et al., 2005), saturation in the retina or LGN (Li et al., 2006; Priebe and Ferster, 2006; Smith et al., 2006) and depression at the thalamo-cortical synapse (Freeman et al., 2002). The last two accounts are applicable only when the mask and test are presented to the same eye (monoptic presentation) and overlap in space and time. However, in cat at least, XOS is not a purely ipsiocular process because when an oriented grating and cross-oriented mask are presented to different eyes (dichoptic presentation), suppression is evident in striate cells (Sengpiel et al., 1995; Walker et al., 1998; Li et al., 2005; Sengpiel and Vorobyov, 2005). Although interocular suppression has been found in the LGN (e.g. Sanderson et al., 1969; Murphy and Sillito, 1989; Felisberti and Derrington, 1999) a cortical origin for dichoptic XOS seems likely since it is diminished when the GABA antagonist bicuculline is used to block intracortical inhibition (Sengpiel and Vorobyov, 2005). These results suggest that at least two mechanisms underlie XOS in cat: a cortical interocular mechanism, and a pre-cortical ipsiocular mechanism.

Cross-orientation masking (XOM) is a phenomenon observed at the behavioral level and is thought to be a consequence of the neural process of XOS (Foley, 1994; Meese and Hess, 2004). With appropriate stimulation, these psychophysical effects can be substantial, raising contrast detection threshold by more than a factor of 4 (Meese and Holmes, 2007). If the dual pathways for XOS in cat are also to be found in primate, then we might expect eye of origin of mask and test gratings to influence human performance. However, most previous studies of XOM have used binocular presentation (e.g. Foley, 1994; Meese and Holmes, 2007), which one might suppose combines masking influences from both within and between the eyes (though see Discussion). Few studies have attempted to separate the two, and those that have (e.g. Legge, 1979; Levi et al., 1979; Meese and Hess, 2004) did not provide a detailed comparison of monoptic and dichoptic XOM func-

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Abbreviations: LGN, lateral geniculate nucleus; RMS, root mean square; S.E., standard error; V1, visual area 1; XOM, cross-orientation masking; XOS, cross-orientation suppression.

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tions. We address this here with the specific aim of investigating the number of pathways involved in human XOM.

EXPERIMENTAL PROCEDURES

Equipment and observers

Stimuli were displayed on a Clinton Monoray monitor with a frame rate of 120 Hz using a Cambridge Research Systems ViSaGe stimulus generator controlled by a desktop computer and were viewed through a mirror stereoscope (Cambridge Research Systems, Rochester, Kent, UK). A central fixation point was present throughout, and stimuli were displayed in the center of a circular aperture with a diameter of 9° and a dark surround, at an optical viewing distance of 57 cm. Mean luminance of the central display region was 30 cd/m^2 after attenuation by a neutral density filter. The display was gamma corrected to ensure linearity over the full contrast range, and a frame interleaving technique (60 Hz per image) was used for all conditions, allowing the contrasts of the mask and test stimuli to be varied independently using lookup tables.

The three observers were all psychophysically experienced and wore their normal optical correction.

Stimuli

Mask and test stimuli were circular patches of sinusoidal grating, spatially modulated by a raised cosine window (see inset to Fig. 2), with a central plateau 3° in diameter. Test gratings were always horizontal and had a spatial frequency of 1 c/°. Two different cross-oriented mask gratings were used. One was a vertical grating (oriented perpendicular to the test) with a spatial frequency of 1 c/°. The other was an oblique grating (−45°) with a spatial frequency of 3 c/°. The first arrangement is a canonical stimulus for XOM and uses mask and test spatial frequencies that are known to produce large effects (Meese and Holmes, 2007). The second extends the stimulus space in spatial frequency and orientation and helps place the present study within a larger body of ongoing psychophysical work (Meese and Holmes, 2002; Meese, 2004; Meese and Hess, 2004; Meese et al., in press).

There were two ocular conditions for each type of mask. In the monoptic condition, the mask and test were presented to the same eye and the other eye was presented with mean luminance. In the dichoptic condition the mask and test were presented to different eyes. (A third, 'half-binocular,' condition is described in the Discussion.) On each trial, the spatial phase of the mask and the test was randomly selected from one of four values (0, 90, 180 or 270°) to homogenize local luminance adaptation. Stimulus contrast is expressed as Michelson contrast in percent, given by $c=100(L_{max}-L_{min})/(L_{max}+L_{min})$.

In experiments I and II, detection thresholds were measured for all four mask/test configurations. These experiments explored the effects of stimulus duration (25–400 ms) and mask contrast (0%–45%), respectively. The mask and test were always superimposed in time and had the same duration. Experiment III used an adaptation paradigm, in which the mask eye was presented with an adapting pattern for 2 min. This was a vertical 1 c/° grating with contrast of either 0% or 50%. To evenly distribute local luminance adaptation, the phase of the adaptor was shifted by 90+x° every 100 ms, where x was a value randomly selected from the range 0–180°. Top-up adaptation periods of 6 s occurred before each trial and were followed by a blank period of 500 ms before the first test interval.

In all three experiments, monoptic detection thresholds were also gathered in the absence of a mask (a no-mask control condition). In experiment II, binocular detection thresholds were also measured for a mask contrast of 0%. This was to help specify some of the model parameters as described in Appendix A.

Procedure

Subjects were seated in a dark room with their heads in a support to which the stereoscope was attached. A two-interval forced-choice (2IFC) procedure was used to estimate detection thresholds (interstimulus interval=500 ms). One interval contained only the mask grating, and the other contained the mask plus the test grating. Subjects indicated which interval contained the test grating by pressing one of two mouse buttons and auditory feedback indicated correctness of response. Stimulus conditions were blocked by mask contrast level, duration and mask type (i.e. 1 c/° or 3 c/°). Within each block, the monoptic and dichoptic conditions were randomly interleaved across trials. For each condition, a pair of three-down, one-up staircases was used (Wetherill and Levitt, 1965), where the target contrast was decreased after three consecutive correct responses and increased after a single incorrect response. For each staircase, the contrast step-size began at 12 dB (a factor of 4), but decreased to 3 dB (a factor of $\sqrt{2}$) after the initial reversal in staircase direction. Each staircase terminated after 12 subsequent reversals in direction (typically about 47 trials), and only the data gathered during this stage were used in the analysis. In experiments I and II the two staircases in a pair tracked thresholds for complementary conditions across eye and were randomly interleaved. In experiment III, just one eye was adapted on each day of experimentation. The mask was presented to the adapted eye, and the test was presented to either the same eye (monoptic) or the other eye (dichoptic). In all experiments, results were similar for the complementary conditions and so the data for each condition of interest (no-mask, monoptic mask, dichoptic mask) were collapsed across the eye tested. Each observer repeated the experiment four times, and thresholds (75% correct) and standard errors (S.E.) were calculated by probit analysis after collapsing the data across replication. This produced individual threshold estimates for each observer based on about 375 trials.

The block length of experimental sessions (a single mask contrast) varied across experiments and conditions (e.g. stimulus duration), but was typically between 5 and 20 min. Thus, we cannot rule out the possibility that there was a small buildup of adaptation to the briefly presented (≤400 ms) masks. Our use of a blocked design means that high contrast masks are unlikely to have interfered with lower contrast masks (as they might in an intermixed design), but it is possible that the effective masking contrast might have been attenuated, similar to compressing the mask contrast axis slightly in Fig. 5. A further advantage of the blocked design over the intermixed design is that observers were able to attend to the appropriate visual cue for each condition, thus reducing potentially confounding effects of uncertainty (e.g. the visual cue for a horizontal grating target without a mask can be very different from that in the presence of a high contrast vertical mask).

RESULTS

Qualitative model predictions

Four possible arrangements for XOS are shown in Fig. 1, where the models are devised to operate around psychophysical detection threshold. We consider the situations where the test grating is presented to one eye (it does not matter which, hence icons are shown for both eyes) and the mask is also presented to only one eye which is either the same (monoptic) or different (dichoptic) from the test. In principle, masking from monoptic and dichoptic stimuli could be due to a common mechanism at a purely binocular site. This is shown in Model 1 (Fig. 1a), where XOS is placed after binocular summation. In this case, the contrast