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Retinal visual processing constrains human ocular following response

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ABSTRACT

Ocular following responses (OFRs) are the initial tracking eye movements elicited at ultra-short latency by sudden motion of a textured pattern. We wished to evaluate quantitatively the impact that subcortical stages of visual processing might have on the OFRs. In three experiments we recorded the OFRs of human subjects to brief horizontal motion of 1D vertical sine-wave gratings restricted to an elongated horizontal aperture. Gratings were composed of a variable number of abutting horizontal strips where alternate strips were in counterphase. In one of the experiments we also utilized gratings occupying a variable number of horizontal strips separated vertically by mean-luminance gaps. We modeled retinal center/surround receptive fields as a difference of two 2-D Gaussian functions. When the characteristics of such local filters were selected in accord with the known properties of primate retinal ganglion cells, a single-layer model was capable to quantitatively account for the observed changes in the OFR amplitude for stimuli composed of counterphase strips of different heights (Experiment 1), for a wide range of stimulus contrasts (Experiment 2) and spatial frequencies (Experiment 3). A similar model using oriented filters that resemble cortical simple cells was also able to account for these data. Since similar filters can be constructed from the linear summation of retinal filters, and these filters alone can explain the data, we conclude that retinal processing determines the response to these stimuli. Thus, with appropriately chosen stimuli, OFRs can be used to study visual spatial integration processes as early as in the retina.
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1. Introduction

The ocular following response (OFR) is the initial tracking movement of the eyes elicited at ultra-short latency by the motion of a textured pattern (see Miles, 1998 for review). Early work has concentrated on elucidating its role in gaze stabilization (Busettini, Miles, & Schwarz, 1991; Gellman, Carl, & Miles, 1990; Masson et al., 2001; Miles & Kawano, 1986; Miles, Kawano, & Optican, 1986). However, over the years the OFR has also emerged as a powerful behavioral probe for studying the early stages of cortical visual motion processing (Kodaka et al., 2007; Miles & Sheliga, 2009).

An extensive body of evidence has been accumulated about cortical direction-selective neuronal machinery that mediates the OFR (see Masson & Perrinet, 2012 for review). However, visual stimuli are processed in the retinogeniculate pathway before direction selectivity appears (in the striate cortex), so in this paper we develop a stimulus intended to probe the contribution of these early processes to the OFR. Fig. 1 illustrates the principle that we exploit in this study. It depicts 1-D vertical sinewave gratings. In panels A and B the grating consists of a series of abutting strips in which alternate strips are in counterphase. Panel C illustrates the stimulus that results if all strips are in phase. Several key properties of stimuli in Fig. 1 are the same: the total area occupied, the horizontal and vertical extent, the contrast, the distribution of pixel luminance values. The processing of these stimuli in the visual system, however, could result in quite different outcomes. Schematics of two filters—like a 2-D on-center/off-surround classical receptive field (RF) of retinal ganglion cells—are superimposed onto each panel of Fig. 1. The size of the lower filter in each pair is substantially larger than the upper one. The output of the lower filter would be close to maximum for the stimuli shown in panels B and C, where as it would be negligible for the stimulus shown in panel A, because in the latter case the dark and bright areas of the grating would largely cancel each other in the on-center as well as in the off-surround of the filter. If such stimuli were subjected to motion, the cortical motion-sensitive circuits would be fed by a strong filter output in cases B and C but not in case A. In contrast, for the smaller upper filter—shown also in a magnified view to the right of Fig. 1 panels—the filter output would be the strongest in case A, weaker in case B, and the weakest in case C. In this study we develop a simple model using antagonistic center/surround filters, with properties selected in accord with the known properties of primate retinal ganglion cells. This simple model was able to *quantitatively* account for the observed changes in the OFR

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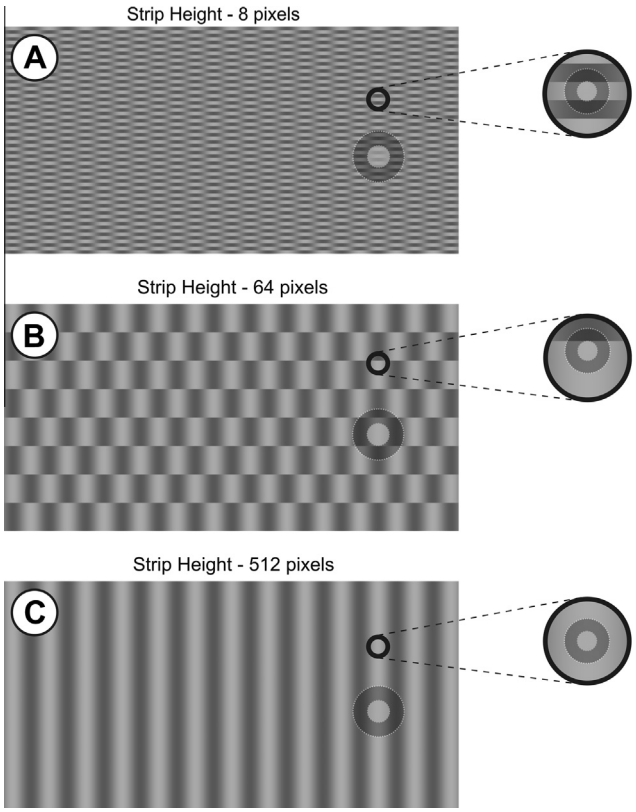

Fig. 1. Stimulus spatial layout in Experiment 1. Gratings were confined to a single rectangular region composed of a variable number of abutting equal-height horizontal strips such that the neighboring strips were always in counterphase. Gratings shown are scaled versions of 0.25 cpd 32% contrast stimuli. The height of a strip equaled ~0.1 times (A; 8 pixels), ~0.78 times (B; 64 pixels), and ~6.23 times (C; 512 pixels) the grating wavelength. Schematics of two 2-D on-center/off-surround classical receptive fields of retinal ganglion cells are superimposed onto the stimuli in each panel: the size of the lower filter in each pair is substantially larger than the upper one. The output of the lower filter would be close to maximum for the stimuli shown in panels (B) and (C), where as it would be negligible for the stimulus shown in panel (A), because in the latter case the dark and bright areas of the grating would largely cancel each other in the on-center as well as in the off-surround of the filter. Conversely, for the smaller upper filter—shown also in a magnified view to the right of panels—the filter output would be the strongest in case (A), weaker in case (B), and the weakest in case (C).

amplitude for stimuli composed of counterphase strips of different heights (Experiment 1), for a wide range of stimulus contrasts (Experiment 2) and spatial frequencies (Experiment 3).

Some preliminary results of this study were presented in abstract form elsewhere (Sheliga, Quaia, & FitzGibbon, 2011).

2. Experiment 1: OFRs to gratings comprised of counterphase horizontal strips of variable height

2.1. Material and methods

Most of the techniques were very similar to those used previously in our laboratory (Sheliga et al., 2005, 2012) and, therefore, will only be described in brief here. Experimental protocols were approved by the Institutional Review Committee concerned with the use of human subjects.

2.1.1. Subjects

Three subjects participated in this study: two were authors (BMS and EJF) and the third was a paid volunteer who was unaware of the purpose of the experiments (AGB). All subjects had normal or corrected-to-normal vision. Viewing was binocular.

2.1.2. Eye-movement recording

The horizontal and vertical positions of one eye (right eye in BMS and EJF; left eye in AGB) were recorded with an electromagnetic induction technique (Robinson, 1963) using a scleral search coil embedded in a silastin ring (Collewijn, Van Der Mark, & Jansen, 1975), as described by Yang, FitzGibbon, and Miles (2003).

2.1.3. Visual display and the grating stimuli

The subjects sat in a dark room with their heads positioned by means of adjustable rests (for the forehead and chin) and secured in place with a head band. Visual stimuli were presented on a 21″ CRT monitor located straight ahead at 45.7 cm from the corneal vertex. The monitor screen was 400 mm wide and 300 mm high, with a resolution of 1024 × 768 pixels (20.55 pixels/°, directly ahead of the eyes), a vertical refresh rate of 160 Hz, and a mean luminance of 20.8 cd/m^2. The RGB signals from the video card provided the inputs to an attenuator (Pelli, 1997) whose output was connected to the RGB inputs of the monitor via a video signal splitter (Black Box Corp., AC085A-R2). This arrangement allowed the presentation of black and white images with 11-bit grayscale resolution.

The visual stimuli consisted of 1-D vertical gratings with sinusoidal luminance profiles (0.25 cpd; 32% contrast) which extended the full width of the display (47°) and underwent successive 1/8-wavelength shifts each video frame (20 Hz temporal frequency). The gratings were ~25° in height and centered vertically at a subject's eye level. On any given trial, gratings were composed of a variable number (from 1 to 128) of abutting equal-height horizontal strips such that the neighboring strips were always in counterphase (180° phase difference). The height of a strip could range from ~0.05 times (~0.2°; 4 pixels) to ~6.23 times (~25°; 512 pixels) the grating wavelength in octave increments. See Fig. 1A–C for examples. Each block of trials had 16 randomly interleaved stimuli: 8 strip heights and 2 directions of motion (leftward vs. rightward).

2.1.4. Procedures

All aspects of the experimental paradigms were controlled by two PCs, which communicated via Ethernet using the TCP/IP protocol. One of the PCs was running a Real-time EXperimentation software package (REX) developed by Hays, Richmond, and Optican (1982), and provided the overall control of the experimental protocol as well as acquiring, displaying, and storing the eye-movement data. The other PC was running Matlab subroutines, utilizing the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997), and generated the visual stimuli.

At the beginning of each trial, the grating patterns appeared (randomly selected from a lookup table) together with a target spot (diameter, 0.25°) at the screen center that the subject was instructed to fixate. After the subject's eye had been positioned within 2° of the fixation target and no saccades had been detected (using an eye velocity threshold of 18°/s) for a randomized period of 600–1100 ms the fixation target disappeared and motion began. The motion lasted for 200 ms, at which point the screen became a uniform gray (luminance, 20.8 cd/m^2) marking the end of the trial. After an inter-trial interval of 500 ms a new grating pattern appeared together with a central fixation target, commencing a new trial. The subjects were asked to refrain from blinking or shifting fixation except during the inter-trial intervals but were given no instructions relating to the motion stimuli. If no saccades were detected for the duration of the trial, then the data were stored to disk; otherwise, the trial was aborted and subsequently repeated within the same block. Data were collected over several sessions