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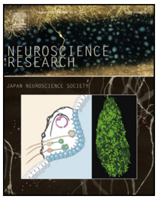

Temporal impulse response function of the visual system estimated from ocular following responses in humans

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ABSTRACT

Early visual processing functions as a set of spatiotemporal image filters. Our ability to sense changes in retinal images is determined by these filters along the temporal axis. In this study, we developed a paradigm to identify the kernel of the temporal filters based on ocular following responses (OFRs) to two-frame apparent motion stimuli. We first conducted two experiments to acquire fundamental data. In the first experiment, in which a quarter wavelength step of a sinusoidal grating was presented with various inter-stimulus intervals (ISIs), we found that OFRs were reversed by the ISI, which is consistent with previous findings. In the second experiment, a quarter wavelength step of a sinusoidal grating was applied with various durations of the initial image frame (motion onset delays; MODs); we found that longer exposure to the initial image reduced OFRs. Parameters of motion energy model involving temporal filters were optimized so that the model could reproduce the dependence of OFRs on ISIs and MODs. We were then able to successfully obtain quantitative estimates of the biphasic temporal filters with optimal frequencies in 6–8 Hz. This method is completely objective and will thus be applicable to a wide range of human subjects and model animals.

1. Introduction

Early visual processing functions as a set of spatiotemporal image filters whose characteristics determine what/how we can see. Our ability to sense changes in retinal images is determined by filters in the temporal domain. Critical flicker (-fusion) frequency (CFF) is the highest temporal frequency of images that we can perceive changes in brightness. Thus, it is one of the measures used to describe the characteristics of the temporal filter. Contrast sensitivity (or threshold) to the flickering of images at different temporal frequencies reveals the frequency characteristics of temporal filters (Kelly, 1961a). The impulse response function of the temporal filter has been quantitatively reconstructed based on a model consisting of linear photoreactive and pulse-encoding stages (Kelly, 1961b). The temporal filter kernels have also been quantitatively estimated using double-step methods (Burr and Morrone, 1993; Hisakata and Murakami, 2008).

Two frame animations presented with inter-stimulus intervals (ISIs) induce reversed motion percepts. Shioiri and Cavanagh (1990) have suggested that this phenomenon is due to the characteristics of the temporal filters embedded in the visual system. The energy-based motion detector of Adelson and Bergen (1985) involves temporal filters with biphasic impulse response functions. This model can at least qualitatively explain the existence of illusory motion percepts in ISI experiments (Strout et al., 1994; Takeuchi and De Valois, 1997). Recently, the temporal filters have been quantitatively estimated from perceived motions using this motion energy model (Challinor and Mather, 2010). Thus, illusory motion percepts also provide clues to the nature of temporal filters. However, all of these attempts were based on subjective reports of observers.

Sudden motions of wide-field textures elicit reflexive eye movement responses. Such responses are called ocular following responses (OFRs) (Gellman et al., 1990; Miles et al., 1986). It was suggested that low-level energy-based mechanisms of visual motion detection underlie OFRs (Miura et al., 2006; Sheliga et al., 2005). Two frame animations presented with ISIs induced OFRs in the reversed direction, as was observed with motion percepts (Nohara et al., 2015; Sheliga et al., 2006). Researchers then argued that the reversed responses are consistent with the biphasic impulse response functions of temporal filters. Since the OFRs are

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purely reflexive, the responses may be used as an objective measure to quantitatively identify the temporal filters in early visual processing, though there were some different response characteristics between motion perception and OFRs (Nohara et al., 2015; Sheliga et al., 2006). However, no studies have been devoted to deriving quantitative estimates of the temporal filters for the OFRs to the two-frame motion.

Here we report the development of an experimental paradigm to identify the kernel of the temporal filters based on OFRs to two-frame apparent motion stimuli. We first established a simple but novel experimental procedure to study the process of temporal filtering of images using OFRs. We then quantitatively estimated the temporal filters applied to images based on the observed data under the assumption that a motion energy model proposed by Adelson and Bergen (1985) underlies the OFRs. We compared our findings to previous findings and considered our paradigm's methodological benefits and limitations.

2. Materials and methods

2.1. Subjects

Eye movements were recorded from two subjects (S1 and S2, aged 29 and 44, respectively). S1 was naïve and unaware of the experimental design, and S2 was one of the authors. Each subject had normal or corrected-to-normal vision, normal visual fields, and clinically normal eye movements. CFFs were measured using T.K.K.501c (Takei Scientific Instruments Co. Ltd., Niigata, Japan) and estimated to be 38.1 and 36.0 Hz for S1 and S2, respectively. Informed consent, based on the Helsinki Declaration, was obtained from each subject. All experimental procedures were approved by the Kyoto University Graduate School and Faculty of Medicine Ethics Committee.

2.2. Visual display

The visual apparatus was similar to that used in our previous study (Miura et al., 2009). The subjects faced a 19-in. CRT monitor Eizo T766, positioned 63.4 cm in front of the eyes in a dark room. Visual stimuli were presented on the monitor (resolution, 1280 × 960 pixels; vertical refresh rate, 100 Hz). The subjects viewed the visual stimuli binocularly. RGB signals from the video card were converted to gray scale images with 11-bit resolution through an attenuator (Pelli and Zhang, 1991). A luminance lookup table with 256 luminance levels equally spaced from 0.0 to 10.0 cd/m^2 was created using direct luminance measurements (LS-100 photometer; Konica-Minolta, Japan) under software control. This table was then expanded to include 2048 equally spaced levels by interpolation.

2.3. Visual stimulus and procedures

We used the two-frame apparent motion of a vertical sinusoidal grating with a spatial frequency of 0.25 cycles/°, a Michelson contrast of 32%, and a mean luminance of 5.0 cd/m^2. We used this setting because the optimal spatial frequency for eye movement responses was about 0.25 cycles/° (Miura et al., 2009; Sheliga et al., 2005). We carried out two experiments using two-frame apparent motion of the sinusoidal grating patterns.

2.3.1. Experiment 1

At the beginning of each trial, a fixation target with a diameter of 0.5° appeared. The subjects were instructed to look at the fixation target. After the right eye was positioned within ±2° from the fixation target for a randomized period between 500 and 1000 ms, a sinusoidal grating appeared behind the fixation target. The initial phase of the sinusoidal grating was randomized from trial to trial at intervals of 1/8 of a wavelength. The subjects fixated on the target for a further 320 ms. The grating pattern was then replaced by a uniform gray image with a mean luminance the same as that of the former pattern (ISI). The ISI was set to 0, 10, 20, 30, 40, 60, 80, 160, 320 or 640 ms. The fixation target was then turned off and the second grating pattern, which was shifted from the initial grating by 1/4 of a wavelength rightward or leftward, appeared. The second frame was presented for 200 ms, after which the image was again replaced by a uniform gray with a mean luminance. This indicated the end of the trial. The next trial started one second after the end of the second frame. The subject was instructed only to fixate the fixation target when it was presented.

2.3.2. Experiment 2

At the beginning of each trial, a fixation target with a diameter of 0.5° appeared. After the right eye was positioned within ±2° of the fixation target for a randomized period between 500 and 1000 ms, a sinusoidal grating appeared behind the fixation target. After a delay of 0, 10, 20, 30, 40, 60, 80, 160, 320, or 640 ms, the fixation target was turned off. Simultaneously, the second grating, which was shifted rightward or leftward from the initial grating by ¼ of a wavelength, appeared. We call this delay motion onset delay (MOD), as was done in the smooth pursuit experiments of Krauzlis and Lisberger (1994), who used this term to describe the interval between the appearance and the onset of motion of the small pursuit target. The second frame was presented for 200 ms, after which the image was replaced by a uniform gray with the same mean luminance, which indicated the end of the trial. The next trial started one second after the end of the second frame. The instruction to the subject was the same as in experiment 1.

2.4. Data collection and analyses

All aspects of the experimental paradigm were controlled by two computers, as in previous studies (Miura et al., 2006, 2009). One computer ran the Real-time EXperimentation software package (REX) (Hays et al., 1982) for overall experimental protocol control; display, and data acquisition/storage. The other computer ran MATLAB (The Mathworks, MA) with the Psychophysics Toolbox extensions (Brainard, 1997) and generated the visual stimuli upon receiving a start signal from the REX machine.

Eye movements of the right eye were measured using a dual-Purkinje-image eye tracker system (Fourward Technology, VA, USA). Voltage signals encoding the horizontal and vertical components of the eye position were passed through an analog low-pass filter (−3 dB at 200 Hz) and digitized to a resolution of 12 bits, with sampling at 1 kHz. All data were stored and transferred to another PC for analysis using computer programs based on MATLAB. The eye-position data were smoothed using a 4-pole digital Butterworth filter (−3 dB at 25 Hz) and eye-velocity traces were derived from their two-point backward difference. Eye acceleration profiles were derived from the two-point backward difference of the eye-velocity traces and were used to detect saccades during the trials.

Our data analyses were restricted to ocular responses during the initial open loop periods. Changes in horizontal eye position were calculated during 80-ms periods beginning 80 ms after the onset of the second pattern, as the minimum latency of the ocular responses was ~80 ms. For the ISI or MOD stimulus condition, mean responses to leftward motion were subtracted from those to rightward motion to obtain response measures with better signal-to-noise ratios (S/N ratios). We also calculated 95% confidence intervals of the differences to evaluate statistical significance. Based on our convention (rightward positive), ocular responses in the direction of the phase shift were positive, while those in the