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RESEARCH NOTE

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Properties of pupillary responses to dynamic random-dot stereograms

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Abstract Pupillary response can be elicited by a number of visual stimuli. In the present experiments, the pupillary responses to stereo gratings with various spatial frequencies and disparity amplitudes were measured. The spatial frequency was from 0.1 to 1.2 cycles per degree (cpd), and the disparity amplitude was from 4 to 24 min arc. The results showed that pupillary responses can be elicited by all these stereo gratings except when either the spatial frequency or disparity amplitude was reduced to zero. When the disparity amplitude was fixed to 8 min arc, the pupillary response amplitude increased with increasing spatial frequency, eventually reaching a plateau. While the spatial frequency was fixed to 0.3 cpd, the pupillary response amplitude continued to increase within the range of disparity amplitude. This provides a different approach to demonstrate that these pupillary responses were induced by stereo information. In addition, the stereo pupillary responses may be further developed as an objective method to study stereopsis. Finally, plausible underlying mechanisms of the stereo pupillary response are discussed.

Keywords Pupillary response · Stereopsis · Stereo vision · Stereo grating · Disparity amplitude

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Introduction

The pupil is well known for its light reflex (Davson 1990). With the help of advanced pupillometer, it was found that the pupillary response could also be evoked by various visual stimuli, including changes in pattern structure, color content, and motion coherence (Drew et al. 2001; Hung and Sun 1988; Sahraie and Barbur 1997; Sun et al. 1981, 1995, 1998a, b; Ukai 1985; Young and Alpern 1980). The ample visual inputs to the pupil system made the pupillary response a valuable approach for the physiological, pathological, and clinical investigations of human vision (Barbur et al. 1999; Sahraie et al. 2002; Slooter and von Norren 1980; Weiskrantz et al. 1998).

A preliminary result of pupillary response to stereoscopic stimulus with fixed spatial frequency and disparity amplitude was recently reported (Li and Sun 2005). In the present study, stereo pupillary responses to different spatial frequencies and disparity amplitudes are measured, and plausible mechanisms underlying the stereo pupillary response are discussed.

Materials and methods

The present experiment contains two steps. First, pupillary responses to stereo gratings with various spatial frequencies were measured. Next, pupillary responses to various disparity amplitudes were examined.

Stimulus

General description

The stimuli were dynamic random-dot stereograms (Julesz 1971) of 600 dots width by 300 dots height (bright dot, $2' \times 2'$, 60 cd m^{-2}, 20% of density; dark background, 0.05 cd m^{-2}), which were displayed on a 21-inch VDT monitor (G520, Sony) placed 57 cm in front of the subject, at a frame rate of 120 Hz. Each pair of stereograms was composed of two successive frames of random-dot patterns. The odd frames were presented to the left eye and the even frames to the right eye by means of a pair of liquid crystal shutter glasses, which were synchronized with the vertical blanking signals of the VDT. The random-dot patterns in successive frames for each eye were changed randomly, while the disparities between the two eyes were maintained to provide the perception of either a flat surface in the front parallel plane or a stationary sinusoidal grating in depth (Li and Sun 2005; Schumer and Ganz 1979) (Fig. 1a).

Stereo gratings of various spatial frequencies

Sinusoidally modulated stereo gratings with horizontally oriented spatial frequencies of 0.1, 0.4, 0.8, or 1.2 (cpd) were used. The disparity amplitude of these gratings was 8′, with a mean disparity lying in the uncrossed plane at 8′.

Stereo gratings of various disparity amplitudes

Sinusoidally modulated stereo gratings with disparity amplitudes of 4′, 8′, 16′, or 24′ were employed. The mean disparity of these gratings was in the uncrossed plane at 4′, 8′, 16′, or 24′, respectively, to make the perceived grating peaks located at the screen plane (also the fixation plane). The spatial frequency of these gratings was 0.3 cpd in the horizontal direction.

As the control, stereo gratings with 0 cpd spatial frequency or with 0′ disparity amplitude were also tested.

Procedure

Examination of pupillary responses to various spatial frequencies

The time duration for each trial was 3 s. In the beginning of a trial, the flat surface of dynamic random-dots was presented to the subject for 0.5 s. Then, the stimulus was switched to the stereo grating (Fig. 1a). Each session was composed of five successive trials. In each session, stereo gratings with spatial frequencies of 0, 0.1, 0.4, 0.8, and 1.2 cpd were presented in separate trials, in a random sequence. Thirty sessions consisted a block. It took about 60 min to complete a block. On each test day, one block was executed on one subject. A total of three blocks were carried out for each subject. During the experiments, the subject was instructed to fixate a small red fixation mark (20′ in size) located at the center of the VDT screen, with his head held by a chin-and-forehead rest. The pupillary responses and eye movements were recorded simultaneously by an infrared pupillometer (Sun et al. 1979, 1981, 1998b).

Examination of pupillary responses to various disparity amplitudes

The procedure in this step was similar to that in the previous step with the only exception that, in each session, stereo gratings with different disparity amplitudes of 0′, 4′, 8′, 16′, and 24′ were presented.

Subjects

Five volunteers with normal or corrected-to-normal visual acuity and normal stereo vision participated in the present experiments. The experimental protocol was approved by the local ethical committee and followed the tenets of the Declaration of Helsinki. Each subject provided signed written consent before the experiments.

Results

Pupillary responses to various spatial frequencies

The pupillary responses to stereo gratings with various spatial frequencies but fixed disparity amplitude are shown in Fig. 1b (second to fifth traces). The pupillary response amplitude is plotted against the spatial frequency in Fig. 1d. When disparity amplitude was fixed to 8′, the pupillary response increased with increasing spatial frequency from 0.1 to 0.8 cpd. With frequency greater than 0.8 cpd, the pupillary response amplitude ceased increasing and maintained to a platform level. Moreover, with a spatial frequency of zero, no pupillary response was observed (Fig. 1b, first trace). In contrast to the remarkable variation in response amplitude, the latencies of the stereo pupillary responses were nearly constant and around 500–600 ms (Fig. 1f). These results were exhibited in four of five subjects. The exception was subject HMF, who showed no obvious pupillary response for all these spatial frequency stimuli.

Pupillary responses to various disparity amplitudes

When stereo gratings with various disparity amplitudes but fixed spatial frequency were presented to the subject, explicit pupillary responses were elicited (Fig. 1c, second to fifth traces). The pupillary response amplitude is plotted against the disparity amplitude in Fig. 1e. While the spatial frequency was fixed to 0.3 cpd, larger disparity amplitudes usually evoked a larger response and smaller amplitudes always resulted in a smaller response. When the disparity amplitude became zero, no pupillary response was found (Fig. 1c, first trace). The latencies of the stereo pupillary responses to different disparity amplitudes were also nearly constant and around 500–600 ms (Fig. 1 g).

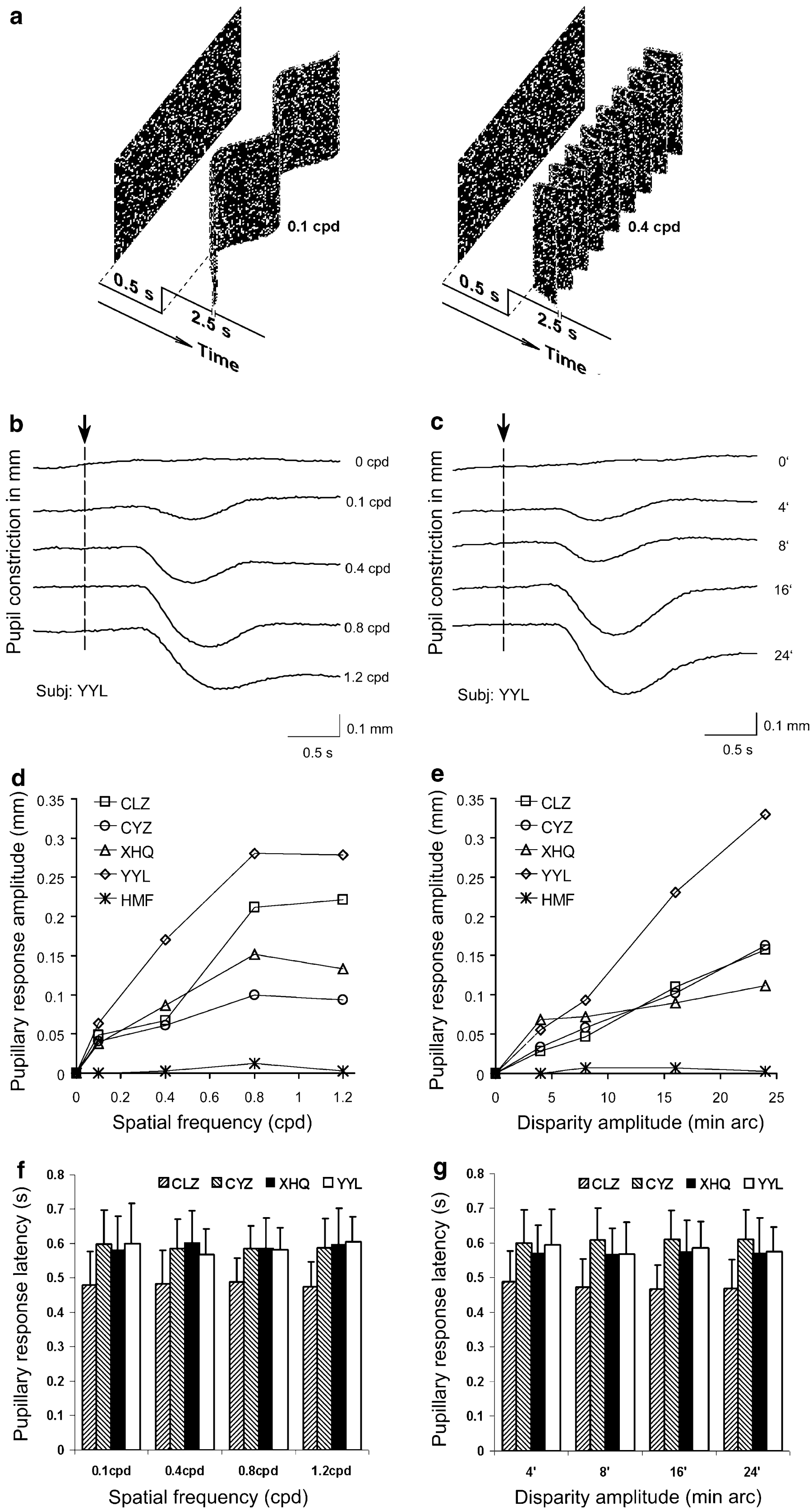

Fig. 1 The schematic diagram for the visual stimuli and the main results of the pupillary responses. **a** Schematic diagram of the stereo stimuli. In the first 0.5 s of a trial, a flat surface was presented to the subject, then, the stimulus switched to a stereo grating and lasted for 2.5 s. Stereo gratings with different spatial frequencies are depicted. **b** Pupillary responses to stereo gratings with various spatial frequencies. *Short arrow* indicates the onset of the stereo grating. Spatial frequencies labeled at *right*. Disparity amplitude, 8′. Each trace averaged from 90 trials. *Calibration bars* are shown at the *bottom-right* of the panel. **c** Pupillary responses to stereo gratings with various disparity amplitudes. Spatial frequency, 0.3 cpd. All labels as panel **b**. **d** Stereo pupillary response amplitude versus spatial frequency. Each symbol represents one subject; each data point averaged from 90 trials. **e** Stereo pupillary response amplitude versus disparity amplitude. All labels as panel **d**. **f** Stereo pupillary response latency versus spatial frequency. Each *fill pattern* represents one subject. The *short bar* indicates the standard error. **g** Stereo pupillary response latency versus disparity amplitude. All labels as panel **f**

Discussion

Pupillary response could be evoked by binocular rather than monocular viewing of stereoscopic stimulus, implying that the pupillary response could be induced by stereo information (Li and Sun 2005). The present experimental results further showed that explicit pupillary responses were elicited by different spatial frequencies and disparity amplitudes rather than zero frequency or zero disparity. Actually, in either the zero frequency or zero disparity condition, the stereo grating was degenerated into a flat surface without any stereo information. Thus, the present results provide a new approach to demonstrate that these pupillary responses were induced by stereo information.

The pupil is sensitive to oculomovements (Davson 1990), so it should be considered whether the stereo pupillary responses were produced by accommodation changes or the pupil near reflex. First, the accommodation changes could be excluded because the amplitude of stereo pupillary response varied with the spatial frequency (Fig. 1d), and this response was never found in monocular view conditions (Li and Sun 2005). Second, the pupil near reflex could not account for the stereo pupillary response either, because no obvious changes were found in the simultaneous recording of eye movements (Li and Sun 2005). In addition, the stereo stimuli employed in these experiments contained only the uncrossed disparities, which were more likely to induce the divergence rather than convergence eye movements. And, the divergence, in turn, could only result in pupillary dilation (Davson 1990).

The amplitude of the stereo pupillary response increased rapidly with the spatial frequency from 0.1 to 0.8 cpd and then maintained to a platform level (Fig. 1d). In comparison, the maximum amplitude of pupillary response to 2-D luminance grating occurred in the range 1–5 cpd (Barbur 1988, 2004). This difference implied that the underlying mechanisms of the two pupillary responses were different, which could also be reflected from their latency difference. The latency of stereo pupillary response was around 500–600 ms (Fig. 1f, g), similar to the latency of pupil motion response but longer than the latencies of pupillary responses to color, 2-D grating, and luminance (Barbur et al. 1998). This relatively long latency suggested that stereo pupillary response might reflect neural activities at a higher stage of the visual hierarchy. A stimulus-specific pupil response hypothesis stated that transient pupillary response could result from sudden activity changes in cortical neurons (see Barbur 2004 for review). Since the disparity-selective neurons exist extensively in visual cortex (Cumming and DeAngelis 2001; Gonzalez and Perez 1998), the presence of the stereoscopic stimuli might cause activity changes in part of these neurons. Thus, this hypothesis provided a plausible explanation for the stereo pupillary response.

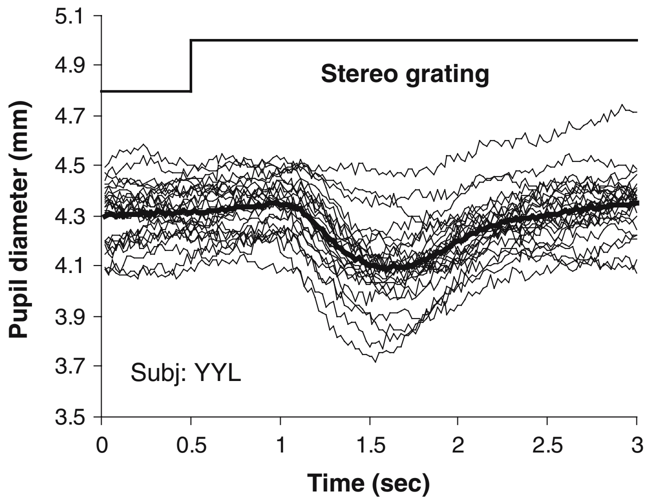

Fig. 2 Single traces of stereo pupillary responses. *Thick curve* indicates the average. The stimulus is a stereo grating with 0.3 cpd spatial frequency and 16′ disparity amplitude

Most examinations of stereo vision are based on the subjective reports with psychophysical methods (Simons 1981a, b). The stereo pupillary response could be developed as an involuntary method for the examination of stereopsis after further systematic investigations in laboratory. As usual with pupil responses, the amplitude of single stereo pupillary responses fluctuated during different runs. As an example, samples of single responses to the same stereo stimulus were shown in Fig. 2. The effect of such fluctuation could be diminished by average method. But the repeated measurements for average were usually time-consuming. Thus, the method to reduce the experimental time would be the major step to overcome when applying the stereo pupillary response to the examination of stereopsis.

During the present experiments, subjects reported clear perception of stereo gratings at all times when the stereo pupillary response was recorded. One exception was the subject HMF who has normal pupillary light reflex and normal stereo vision (stereo acuity of about 30″), and could perceive all the stereo gratings during the experiments, however, no stereo pupillary response was recorded from her during the experiments that she participated in. Clinical examination showed that she has no ocular disease. She also did not take any medicine during the experimental days. This exception suggested that the pupillary experiment and psychophysical test could not supersede each other in the studies of visual perception. Meanwhile, it also might reflect the complexity of pupillary control, which would stimulate further investigation in the pupillary response, such as systematical comparison of the pupillary responses to various visual inputs in a large population of subjects.

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References

Barbur JL (1988) Spatial frequency specific measurements and their use in clinical psychophysics. Clin Vision Sci 2:225–233

Barbur JL (2004) Learning from the pupil—studies of basic mechanisms and clinical applications. In: Chalupa LM, Werner JS (eds) The visual neurosciences. MIT, Cambridge, pp 641–656

Barbur JL, Wolf J, Lennie P (1998) Visual processing levels revealed by response latencies to changes in different visual attributes. Proc R Soc Lond B Biol Sci 265:2321–2325

Barbur JL, Weiskrantz L, Harlow JA (1999) The unseen color aftereffect of an unseen stimulus: insight from blindsight into mechanisms of color afterimages. Proc Natl Acad Sci USA 96:11637–11641

Cumming BG, DeAngelis GC (2001) The physiology of stereopsis. Annu Rev Neurosci 24:203–238

Davson H (1990) The Physiology of the eye. Macmillan, London

Drew P, Sayres R, Watanabe K, Shimojo S (2001) Pupillary response to chromatic flicker. Exp Brain Res 136:256–262

Gonzalez F, Perez R (1998) Neural mechanisms underlying stereoscopic vision. Prog Neurobiol 55:191–224

Hung G, Sun F (1988) Human pupillary response to ramp changes in light intensity. Exp Neurol 100:322–331

Julesz B (1971) Foundations of cyclopean perception. University of Chicago Press, Chicago

Li Z, Sun F (2005) Pupillary response induced by stereoscopic stimuli. Exp Brain Res 160:394–397

Sahraie A, Barbur JL (1997) Pupil response triggered by the onset of coherent motion. Graefes Arch Clin Exp Ophthalmol 235:494–500

Sahraie A, Weiskrantz L, Trevethan CT, Cruce R, Murray AD (2002) Psychophysical and pupillometric study of spatial channels of visual processing in blindsight. Exp Brain Res 143:249–256

Schumer R, Ganz L (1979) Independent stereoscopic channels for different extents of spatial pooling. Vision Res 19:1303–1314

Simons K (1981a) Stereoacuity norms in young children. Arch Ophthalmol 99:439–445

Simons K (1981b) A comparison of the Frisby, Random-Dot E, TNO, and Randot circles stereotests in screening and office use. Arch Ophthalmol 99:446–452

Slooter J, von Norren D (1980) Visual acuity measured with pupil responses to checkerboard stimuli. Invest Ophthalmol Vis Sci 19:105–108

Sun F, Dai S, Zhao X, Qin Y (1979) An infrared instrument television for measurement of dynamic pupil area. Acta Electron Sin 3:63–67

Sun F, Liu H, Liu Y (1981) Dynamic pupillary response to positive differential of light stimulus. Sci Sin 24:872–884

Sun F, Chen L, Zhao X (1995) Transient pupillary responses elicited by displacement of the light spot stimulus. Acta Biophys Sin 11:373–378

Sun F, Chen L, Zhao X (1998a) Pupillary responses evoked by spatial patterns. Acta Physiol Sin 50:67–74

Sun W, Sun F, Hung G (1998b) Neural network mosaic model for pupillary responses to spatial stimuli. Biol Cybern 79:131–138

Ukai K (1985) Spatial pattern as a stimulus to the pupillary system. J Opt Soc Am A 2:1094–1099

Weiskrantz L, Cowey A, Mare CL (1998) Learning from the pupil: a spatial visual channel in the absence of V1 in monkey and human. Brain 121:1065–1072

Young RSL, Alpern M (1980) Pupil responses to foveal exchange of monochromatic lights. J Opt Soc Am 70:697–706