The |L-M| chromatic mechanism in the pupillary pathway

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Recently it has been shown that change in stimulus colour contributes to a pupillary control mechanism. However, the role of pupillary responses to chromatic stimuli is not clear. The aim of this study was to investigate how colour and luminance signals contribute to the pupillary control mechanism. In the first experiment we measured pupillary responses to various colour of stimuli modulated in M- and L-cone contrast space. Iso-response contour in cone-contrast space reflects a possible mechanism which determines the pupillary responses. The results showed that the pupillary iso-response contours were well fitted by a straight line with a positive slope, suggesting that a |L-M| linear chromatic mechanism drives the pupillary responses. In the second experiment we examined spatial and temporal properties of the pupillary responses. We measured the pupillary responses to isoluminant and luminance stimuli at several spatial and temporal frequencies (0.5-8 cycle/deg and 2-32 Hz). The results showed that the pupil response to the chromatic stimulus was larger than that to the luminance stimulus. These results suggested that there are at least two different pupillary control mechanisms for chromatic stimuli and for luminance stimuli, respectively.

Key words*: Pupil response, Cone-contrast space, Luminance mechanism, Chromatic mechanism.*

Introduction

It is widely accepted that pupil responses to visual stimuli are determined by the ambient illuminance. Recently it has been shown that change in stimulus colour also contributes to a pupillary control mechanism (Alpern & Campbell, 1962; Kohn & Clynes, 1969; Kimura & Young, 1995; Tsujimura, Wolffsohn & Gilmartin, 2001, 2003; Babur, 2004 for review). Since both luminance and colour signals drive the pupillary responses, these respective signals should be summed at some point prior to the pupillary control mechanism. However, little is known about how these signals are combined and contribute to the pupillary control mechanism. The aim of this study was to investigate how colour and luminance signals contribute to the pupillary control mechanism.

Methods

Apparatus

The stimulus was generated by a video controller (Cambridge Research Systems, Visage) and displayed on a colour monitor (MITSUBISHI, RDF173H). The resolution of the monitor was 800 x 600 pixels and the frame rate was 140 Hz. Each phosphor was driven by a 15-bit digital-to-analog converter. The monitor was gamma corrected and tested for linearity by using the OPTICAL device provided by Cambridge Research Systems. Cone excitation was calculated according to the spectral radiation of each phosphor, measured by a TOPCON SR-2, using three cone fundamentals obtained by Smith and Pokorny (Smith & Pokorny, 1975).

Measurement of Pupil Size

The pupil of the right eye was imaged using a video camera with a zoom lens located 70 cm away from the

subject and 60° temporal to the visual axis. The video image was fed into an IMAQ PCI-1409 image acquisition board (National Instruments) and analyzed using LabVIEW and IMAQ Vision software at a frequency of 60 Hz. The pupillary response was recorded for 6 s comprising the 2 s test presentation and 2 s pre- and post-task presentations.

Procedure

Three subjects each with normal colour vision and ametropia corrected with ultra-thin hydrophilic contact lenses participated in the experiment. Subjects were seated 64 cm in front of the display monitor. Pupil responses were recorded continuously from the subject's right eye and experimental trials followed an initial adaptation period of 3 minutes.

The presentation sequences of test stimuli were carefully counterbalanced to minimize effects of order of stimulus presentation. Each of the test stimulus presentations were repeated and summed so that each trace represented an average of 30 recordings.

Test stimuli

We generated all stimuli in cone-contrast space. In cone-contrast space we can simply compare the sensitivities of luminance and chromatic stimuli. Comparison of these contrasts is not straight forward as the calculation of chromatic contrast is based on a change in colour whereas the calculation of luminance contrast is based on a change in luminance. In cone-contrast space, the same unit is used to describe the contrast of luminance and chromatic stimuli (*i.e.* cone contrast): hence, we can simply compare the sensitivities of luminance and chromatic stimuli.

Figure 1 represents colours of test gratings in L, M cone-contrast space. In the first experiment, we used 5 different stimuli. The vector directions of these stimuli were 0°-180° (L-cone grating: c-c'), 45°-225° (luminance grating: a-a'), 90°-270° (M-cone grating: d-d'), 117°-297° (red-green isoluminant grating: b-b'), and 153°-333°, respectively. Since any pair of two mixtures with 180-deg difference in their directions are essentially the same stimuli, the measurements can be confined to two quadrants of the cone contrast space. The temporal frequency of the stimulus was 8.0 Hz and the spatial frequency was 1.0 cycle/deg.

In the second experiment we used the luminance stimuli (a-a') and the isoluminant stimuli (b-b') that were modulated at various temporal and spatial frequencies (between 2.0 and 32 Hz for TF and between 0.5 and 8 cycle/deg for SF).

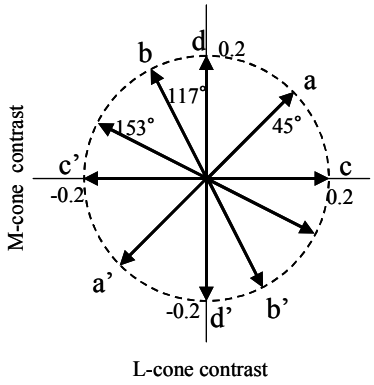

Figure 1. Various colours of test stimuli represented in cone contrast space. In cone contrast space, the vector length defines a stimulus contrast and the vector direction defines a colour.

The vertical sinusoidal gratings were presented in a circular region of 10° diameter at the centre of the screen for 2 s. A yellow background with CIE coordinates (0.40, 0.47) and luminance 27 cd/m² was used throughout. The retinal illuminance of the background was approximately 300 photopic trolands with an average pupil size of 3.8 mm.

Results and Discussion

Experiment 1: Pupillary iso-response contour

Figure 2 shows the pupillary responses evoked by the luminance grating (left panels) and by the red-green isoluminant grating (right panels) for observers HK (upper panels) and NN (lower panels). The response amplitude was recorded as the difference between the initial pupil diameter and the peak constriction. The pupillary responses evoked by the luminance grating

were 0.45 mm for HK, 0.15 mm for NN and 0.20 mm for TM. The responses for the isoluminant grating were 1.1, 0.41 and 0.38 mm, respectively. The pupillary responses evoked by the isoluminant grating were significantly larger than those evoked by the luminance gratings ($P<0.01$ for all subjects). The amplitudes of pupillary responses were different according to the 5 vector directions (45°, 90°, 117°, 153° and 180°) in cone contrast space.

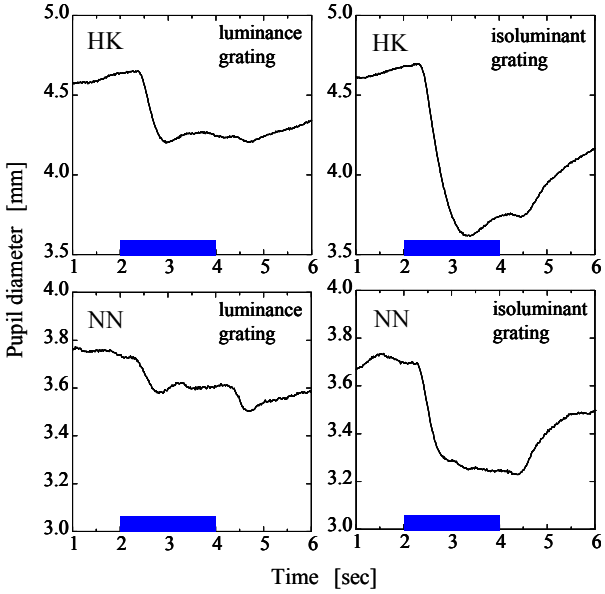

Figure 2. Pupillary responses to luminance and isoluminant stimuli for observers HK (upper panels) and NN (lower panels).

In order to find a relationship between stimulus contrast and pupillary response the pupillary responses to various contrasts (0.08, 0.12, 0.16, and 0.2) along 3 vector directions (90°, 117° and 180°) were measured for all observers in the preliminary experiment. A linear relationship between the test contrast and the amplitude of the pupillary response was found over the range examined (correlation coefficient $r>0.76$ for all observers). The iso-response contrasts (using a criterion of a 0.2 mm change in pupil size) for each vector direction was calculated from the pupillary response evoked by a test grating with a contrast of 0.2. The pupillary iso-response contour in cone-contrast space for observers NN (left panel) and TM (right panel) are shown in Figure 3. Circles represent the iso-response contrasts that induce the same amplitude of pupillary response in each direction. Black circles represent the 90°, 117°, 153° and 180° vector directions (colour gratings) and white circles represent the 45° vector direction (luminance grating). A straight line in each panel represents the best fit line to the data points using a linear least squares method (correlation coefficient $r>0.92$ for all observers).

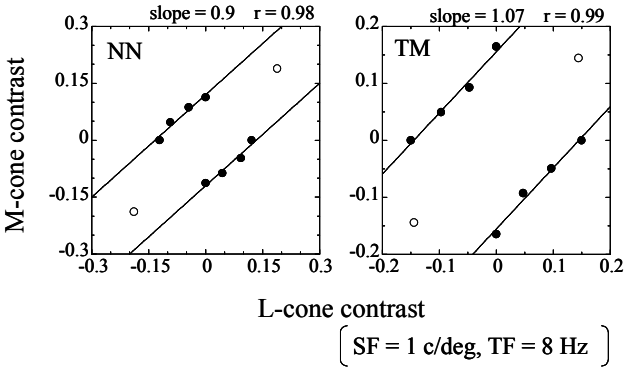

Figure 3. The pupillary iso-response contour for change in pupil diameter of 0.2 mm. The black circles represent iso-response contrasts for various colour gratings and the white circles represent those for the luminance grating. The "r" on the panels represents a correlation coefficient.

The iso-response contour forms a positive slope for all subjects, showing that sensitivities to the chromatic stimuli are higher than those for the luminance stimuli. In other words, it requires a larger stimulus contrast for luminance stimuli to induce a pupillary response of 0.2 mm than that required for chromatic stimuli.

The fact that the isoresponse contour formed the positive slope in M- and L-cone contrast space indicates that a |L-M| chromatic mechanism whereby a signal from L-cone is subtracted from that for the M-cone and *vice versa* drives the pupillary responses.

Experiment 2: Temporal and spatial frequency properties

Figure 4 shows the pupillary response as a function of temporal frequency (a, b) and of spatial frequency (c, d) to the isoluminant stimuli and to the luminance stimuli.

The initial of each observer is at the upper right in the panel. The error bars represent the standard error. The curve of pupillary responses to isoluminant stimuli in each panel represents the best fit curve to the data points using a Difference of two Gaussians (DOG) function. The result showed that pupillary responses to the isoluminant stimuli were larger than that to the luminance stimuli over the range measured. The amplitude of the pupillary responses to isoluminant stimuli varied strongly depending on observers: The pupillary response as a function of TF ranged from 0.33 mm to 1.2 mm for observer HK, ranged from 0.26 mm to 0.58 mm for observer TM, and ranged from 0.18 mm to 0.66 mm for observer NN. The pupillary response as a function of SF ranged from 0.24 mm to 0.34 mm for observer NN, ranged from 0.53 mm to 0.77 mm for observer HK, and ranged from 0.38 mm to 0.59 mm for observer TM.

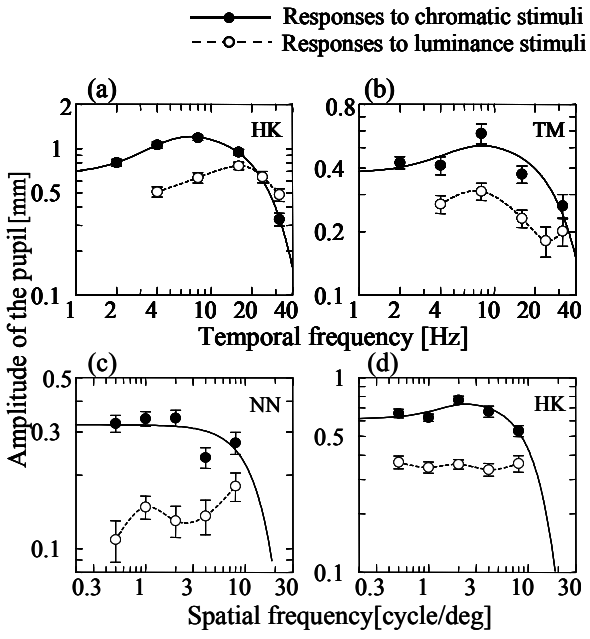

Figure 4. Pupillary responses as a function of temporal frequency (SF = 0 cycle/deg) for observers HK (a) and TM (b). Pupillary responses as a function of spatial frequency (TF = 0 Hz) for observers HK (c) and NN (d).

Interestingly, although the amplitude was different among observers, the shapes of temporal and spatial properties were similar among observers. The amplitudes had a peak at around temporal frequencies between 4 and 10 Hz, and decreased away from the peak. The amplitude has a peak for observers HK and TM at spatial frequencies of 2.0 and 3.0 cycle/deg, whereas it had little variations in low spatial frequencies for observer NN. At high frequencies, the amplitude of pupillary response became smaller across all observers. The pupillary responses to the luminance stimuli, on the other hand, had no systematic change across temporal and spatial frequencies in comparison with those to the isoluminant stimuli.

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