A linear chromatic mechanism drives the pupillary response

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Previous studies have shown that a chromatic mechanism can drive pupil responses. The aim of this research was to clarify whether a linear or nonlinear chromatic mechanism drives pupillary responses by using test stimuli of various colours that are defined in cone contrast space. The pupil and accommodation responses evoked by these test stimuli were continuously and simultaneously objectively measured by photorefractometry. The results with isochromatic and isoluminant stimuli showed that the accommodative level remained approximately constant (< 0.25 D change in mean level) even when the concurrent pupillary response was large (*ca.* 0.30 mm). The pupillary response to an isoluminant grating was sustained, delayed (by *ca.* 60 ms) and larger in amplitude than that for an isochromatic uniform stimulus, which supports previous work suggesting that the chromatic mechanism contributes to the pupillary response. In a second experiment, selected chromatic test gratings were used and isoresponse contours in cone contrast space were obtained. The results showed that the isoresponse contour in cone contrast space is well described ($r^2 = 0.99$) by a straight line with a positive slope. The results indicate that a $|L - M|$ linear chromatic mechanism, whereby a signal from the long wavelength cone is subtracted from that of the middle wavelength cone and vice versa, drives pupillary responses.

Keywords: pupillary response; accommodation response; chromatic mechanism; cone contrast

1. INTRODUCTION

Although most visual information from the eye is directly transmitted to the visual cortex, some is routed to the pre-tectum, which is an area that controls the response characteristics of the pupils. The constriction and dilation of the pupils is evoked by changes in the ambient luminance. However, in addition to changes in retinal illuminance, the response of the pupils to visual stimuli can also be determined by factors such as cognition (Barbur *et al.* 1998) and changes in stimulus colour (Alpern & Campbell 1962; Kohn & Clynes 1969; Young & Alpern 1980; Krastel *et al.* 1985; Barbur *et al.* 1992, 1998; Young *et al.* 1993; Kimura & Young 1995, 1996; Gamlin *et al.* 1998).

The two principal retinocortical pathways, i.e. magnocellular and parvocellular, transmit information on luminance and colour, respectively (e.g. Derrington *et al.* 1984). In order to identify the pathways that contribute to the responses of the pupils, several studies have examined how the pupils respond to specific changes in stimulus attributes, for example their responses to a change in intensity as a function of wavelength (i.e. action spectra) (Alpern & Campbell 1962; Krastel *et al.* 1985; Kimura & Young 1995) and as a function of spatial structure (Ukai 1985) and their responses to movement (Barbur *et al.* 1992). Since it appears that visual attributes are mediated by a specific pathway, they may be useful in identifying the visual pathway that is responsible for the pupils' responses.

In the case of the action spectra, if the magnocellular pathway mediates the information transmitted to the pupils, the pupillary action spectrum has a broadband

property with a single peak in the middle wavelength region. Conversely, if the parvocellular pathway mediates the information, the pupillary responses should have three peaks in the short-, middle- and long-wavelength regions. According to psychophysical theory, a $|L - M|$ chromatic mechanism, whereby a signal from the long wavelength cone (L) is subtracted from that for the middle wavelength cone (M) and vice versa, should have a prominent dip in sensitivity (i.e. a null or a minimum response) at around 570 nm (which is known as the Sloan notch). Some researchers have shown that the pupillary action spectrum has three prominent lobes, which correspond to the observations in psychophysics (Krastel *et al.* 1985; Kimura & Young 1995). In addition, Kimura & Young (1996) measured pupillary responses around the Sloan notch and showed that the responses evoked by a red flash could be neutralized by adding a green flash. These results suggest that a chromatic mechanism contributes to pupillary responses.

If pupillary responses are driven solely by a chromatic mechanism, it should be possible to observe the contribution of the chromatic mechanism independently of the stimulus contrast. However, Kimura & Young's (1996) results showed that the contribution of the chromatic mechanism was only observed at very low contrast near the psychophysical threshold. As the contrast increased, the pupillary action spectrum exhibited a broadband property, with a single peak in the middle wavelength region (i.e. the Sloan notch was not apparent). They also showed that the chromatic cancellation was not present when the contrast was above the threshold. These results suggest that the dominant mechanism that drives pupillary responses is not a chromatic mechanism at contrasts above the threshold. Kimura & Young (1996) theorized that pupillary responses are principally modulated by the chromatic mechanism at low contrasts close to the threshold, whereas above threshold levels, pupillary

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responses are likely to be determined by a compound mechanism with different action spectra (e.g. $|L-M|+|L+M|$). Some researchers (Young & Alpern 1980; Barbur *et al.* 1998) have demonstrated a difference in the latency of pupillary responses between isoluminant and luminance stimuli, thereby suggesting that the balance between the different mechanisms is dependent on visual stimuli.

The aim of this study is to clarify whether a linear (i.e. $|L-M|$) or nonlinear (i.e. $|L-M|+|L+M|$) chromatic mechanism drives pupillary responses by using test stimuli of various colours that are defined in cone contrast space. Of special note is that the test stimuli used for inducing pupil responses were defined in cone contrast space instead of wavelengths. This approach has two benefits. First, as will be described in §2, a pupillary isoresponse contour in cone contrast space was used for identifying which mechanism contributes to the response. If the $|L-M|$ chromatic mechanism drives pupillary responses, the isoresponse contour should form a straight line with a positive slope in cone contrast space (e.g. Chaparro *et al.* 1995). If the $|L+M|$ luminance mechanism drives pupillary responses, the contour should form a straight line with a negative slope (Stromeyer *et al.* 1997; Tsujimura *et al.* 1999, 2000). However, if a nonlinear mechanism drives pupillary responses, the contour will also be nonlinear.

Second, as discussed later, test stimuli around the isoluminant axis are expected to produce much larger responses than around the Sloan notch for a chromatic mechanism, thus improving both the precision of measurement and the ability to isolate the principal mechanism. The chromatic mechanism produces a null (or relatively small) pupillary response around the Sloan notch and so the pupillary response is too small to identify the mechanism involved. Therefore, models based on the Sloan notch have to rely on the assumption that the long wavelength cone and middle wavelength cone signals are linearly subtracted (Kimura & Young 1996).

2. METHODS

(a) Stimulus generation

The stimulus was generated by a video controller (VSG2/3, Cambridge Research Systems, Cambridge, UK) and displayed on a colour monitor (EIZO T68, Kanazawa, Japan). The resolution of the monitor was 640×480 pixels and the frame rate was 150 Hz. Each phosphor was driven by a 12 bit digital-to-analogue converter. Cone excitation was calculated according to the spectral radiation of each phosphor, as measured by a Photo Research PR-650 instrument (Photo Research Inc., Chatsworth, CA, USA), using the three cone fundamentals obtained by Smith & Pokorny (1975).

(b) Colour space

All stimuli were represented in cone contrast space and can be described in the context of cone excitation space. Cone excitation space uses three fundamentals that correspond to the excitation of the three kinds of cone in the retina. The fundamentals were designed so that the total amount of excitation of long wavelength cones and middle wavelength cones is the same as Judd's modified photopic luminosity function $V(\lambda)$ (Smith & Pokorny 1975). These three fundamentals are mapped onto

three orthogonal axes in cone contrast space. A contrast in cone contrast space along each cone axis is defined as

$$C' = \Delta C / C_B, \quad (2.1)$$

where ΔC represents a difference in cone excitation between the background and the test stimulus and C_B represents the cone excitation of the background. Therefore, the origin in cone contrast space represents a background field colour (i.e. yellow in this study). In this experiment, the background colour was kept constant throughout so that cone contrast space was essentially the same as cone excitation space (i.e. it can be linearly transformed to the $(\Delta L, \Delta M, \Delta S)$ space). The short wavelength cone excitation of the test stimulus was also kept constant (i.e. $\Delta S=0$), thereby allowing the data to be plotted in the long wavelength cone and middle wavelength cone contrast spaces, such that the horizontal axis represents a stimulus modulating in the long wavelength cone alone and the vertical axis represents a stimulus modulating in the middle wavelength cone alone. The test stimuli consisted of a combination of the long wavelength cone and middle wavelength cone stimuli with variable amplitude ratios. The vector direction in the space represents the colour of the test stimulus and the vector length represents the stimulus contrast. Therefore, two stimuli that have the same colour but different contrasts can be represented as vectors with the same direction but of different length. The 45° – 225° direction in figure 1 represents the isochromatic axis since the ratio of the long wavelength cone and middle wavelength cone excitations along this axis remains constant and is the same as that of the background (i.e. $L_B/M_B=2.0$). In the first quadrant, the long wavelength cone and middle wavelength cone modulations are in phase, indicating that the stimulus is brighter than the background. Similarly, the stimulus in the third quadrant is darker than the background. The isoluminant axis is represented by the 117° – 297° vector direction. (Note that this is not the 135° – 315° direction since, photometrically, isoluminance is defined as the axis where ΔL is equal to ΔM . Since the L/M ratio of the background is 2.0, the photometrically isoluminant axis should correspond to the direction of $\tan^{-1}(-2.0)$.) The stimulus in the second quadrant appears reddish, whereas that in the fourth quadrant appears greenish since the long wavelength cone and middle wavelength cone modulations are out of phase in these quadrants.

The isoresponse contour of the chromatic mechanism in cone contrast space is expressed as $D = |aL' - bM'|$, where L' and M' are cone contrasts (see equation (2.1)), a and b represent the ratios of the long wavelength cone and middle wavelength cone contrasts to the chromatic mechanism, respectively and D represents the criterion for the response amplitude. The equation describes lines with a positive slope in cone contrast space. Similarly, the isoresponse contour of the luminance mechanism is expressed as $D = |cL' + dM'|$ and describes lines with a negative slope.

(c) Background stimuli

A yellow background with a Commission Internationale de l'Éclairage coordinate of (0.40, 0.47) and a luminance of 34.5 cd m^{-2} was used throughout. The retinal illuminance of the background was *ca.* 2.76 log photopic troland. A yellow background was chosen in order to avoid the effect of short wavelength cone excitation on the pupillary response. The fraction of the background luminance for long wavelength cone contrast (i.e. $r = L_B / (L_B + M_B)$) in the cone excitation diagram proposed

Figure 1. Stimulus representation in the L' and M' cone contrast spaces. Dotted arrows represent the stimuli used in the first experiment and solid arrows the stimuli used in the second experiment. The horizontal axis in cone-contrast space represents a stimulus modulating a long wavelength cone alone and the vertical axis represents a stimulus modulating a medium wavelength cone alone. The test stimuli consisted of a combination of long wavelength and medium wavelength cone stimuli with variable amplitude ratios. The origin in cone contrast space represents a background field colour (i.e. yellow in these experiments). The grating stimuli were symmetrical modulations reflected around the origin, which are represented as **a-a'** or **b-b'**. In a similar fashion, the uniform stimuli are represented as **a** or **b**. The vector length defines the contrast of the stimulus.

by MacLeod & Boynton (1979)) was 0.67 and the ratio of the long wavelength cone and middle wavelength cone excitations was 2.0, being identical to that for 570 nm isochromatic light. The fraction used minimized the apparent variation in the background colour when either the mean luminance level, temporal frequency or spatial frequency of the test grating was changed. Pokorny *et al.* (1993) showed that, for a 570 nm yellow background field, the red:green ratio in flicker detection was approximately constant with respect to changes in the mean luminance. Stromeyer *et al.* (1997) also showed that the ratio of the long wavelength cone and middle wavelength cone inputs to the luminance mechanism were constant with respect to the change in the spatial and temporal frequencies.

(d) Test stimuli

The test stimulus was displayed in a circular region of 10° diameter at the centre of the screen for 2 s. The pupillary and accommodative responses were recorded for an additional 2 s. Two spatial frequencies were used such that the test stimuli appeared uniform ($0 \text{ cycle degree}^{-1}$) or as a grating ($1.6 \text{ cycle degree}^{-1}$). Four test stimuli were used in the first experiment: an isochromatic $1.6 \text{ cycle degree}^{-1}$ bright yellow and dark yellow grating (represented as **a-a'**), an isoluminant $1.6 \text{ cycle degree}^{-1}$ orange and green grating (represented as **b-b'**), a

$0 \text{ cycle degree}^{-1}$ bright yellow uniform stimulus (represented as **a**) and an isoluminant $0 \text{ cycle degree}^{-1}$ green uniform stimulus (represented as **b**) (figure 1). A single contrast (0.16) was used in the first experiment and four contrasts (0.04, 0.08, 0.12 and 0.16) were used in the second experiment in order to investigate the linearity of the pupillary responses over this range. A contrast of 0.16 was chosen, as it was over 20 times greater than the initially measured psychophysical threshold.

(i) Measurement of accommodation and pupil size

The pupil of the right eye was imaged using a video camera (PulnixTM6, Pulnix Europe Ltd, Basingstoke, Hampshire, UK) located 1 m from the subject, 15° temporal to the visual axis. An infrared light source was mounted on the lower half of the video objective, which was masked. The infrared light source produces a gradient of light intensity across the image of the pupil, which is linearly correlated ($r=0.95\text{--}0.99$) with accommodation and can be converted into dioptres following a simple calibration procedure (Schaeffel *et al.* 1993). Changes in pupil size were found not to affect the intensity profile across the pupil significantly in all subjects. The video image was fed into an IMAQ PCI-1407 image acquisition board (National Instruments) and analysed using LABVIEW and IMAQ VISION software (National Instruments, Austin, TX, USA) at a frequency of 50 Hz. The

Figure 2. Pupil and accommodation responses for observer R.C. (*a,b*) The isochromatic test stimuli. (*c,d*) The isoluminant test stimuli. (*a,b*) The grating stimuli ($1.6 \text{ cycle degree}^{-1}$). (*c,d*) The uniform stimuli ($0 \text{ cycle degree}^{-1}$). Each trace represents the average of more than 30 recordings. The onsets and offsets of the test stimuli are shown by the grey boxes on the time-scale axes.

pupil was located using thresholding and edge detection techniques, thereby allowing the pupil diameter to be analysed at a resolution of under 0.01 mm . The gradient of light intensity across the pupil was analysed, thereby allowing the accommodative response to be quantified at a resolution of under 0.05 D .

(ii) Procedure

Six visually corrected (with ultra-thin hydrophilic contact lenses) observers (age range 27.2 ± 3.1 years) participated in the first experiment and four of these observers also participated in the second experiment. The observers were seated 65.7 cm in front of the display monitor and binocularly fixated a black Maltese cross (90% contrast), which subtended 0.8° and was always present in the centre of the screen. The cross acted as an

accommodative 'lock', thereby providing a strong closed-loop stimulus for maintaining the accommodation at a constant level. A session of experimental trials began after an initial adaptation period of 3 min . The pupillary and accommodative responses were continuously recorded from the observer's right eye. Each of the test stimuli presentations was repeated and summed so that each trace represented an average of more than 30 recordings.

3. RESULTS

(a) Pupil and accommodation responses evoked by the isochromatic and isoluminant stimuli

The pupil and accommodation responses evoked by the isochromatic and isoluminant stimuli for observer R. C.,

whose data were typical of all six subjects, are shown in figure 2. All test stimuli produced relatively large pupillary responses (average 0.29 ± 0.16 mm), but did not significantly affect the concurrent accommodative level (difference = 0.00 ± 0.06 and $p = 0.99$). The pupillary response evoked by the isoluminant grating (figure 2c) was slow to re-dilate (i.e. a sustained temporal property), thereby suggesting the involvement of the parvocellular pathway as noted in previous studies (see Gouras 1968; Young & Alpern 1980; Anderson & Burr 1985; Kimura & Young 1995). The isoluminant green uniform stimulus (figure 2d) evoked a large transient response with a secondary dip. This finding is consistent with reported results and has been attributed to after-image cortical mechanisms (Barbur *et al.* 1998, 1999) and to off responses (Kimura & Young 1995).

The finding that the pupillary responses to the isoluminant stimuli were consistently larger for all subjects than those evoked by the isochromatic stimuli runs counter to the widely accepted view that pupillary responses are predominantly driven by the luminance mechanism. It would appear that pupillary responses can be separately driven by both luminance and chromatic stimuli and that, in agreement with psychophysical studies, at lower spatio-temporal frequencies, the sensitivity of pupillary responses to the chromatic mechanism is higher than that for the luminance mechanism. For instance, Stromeyer *et al.* (1995) showed the sensitivity of the chromatic mechanism to be seven times higher than that for the luminance mechanism for detecting a grating at low temporal (1 Hz) and low spatial (1 cycle degree⁻¹) frequencies.

The latency of the pupillary response to the test stimuli was calculated using the normalization technique developed by Barbur *et al.* (1998). The time-courses for the earlier phase of the response (i.e. the time to reach maximum pupil constriction from baseline) were shown to have two characteristics: first, the time-courses were independent of the contrast level after normalization and, second, the time-courses were equivalent for within-class variations in the stimulus level (e.g. contrast), but different for between-class variations in the stimulus level (e.g. uniform colour field and luminance gratings). The amplitudes of the pupillary responses to the isoluminant grating and isochromatic uniform stimuli were normalized with respect to the average amplitude and the traces overlaid such that differences in latency could be detected. Figure 3 shows the onset latencies for observers M. C. and V. P. The latencies for the isoluminant grating stimuli were significantly longer (the differences for each of the subjects were -28.2, 65.5, 65.6, 79.8, 88.1 and 98.4 ms) ($p < 0.05$), on average by 62 ms, than those found for the isochromatic uniform stimulus and were similar to those reported by Barbur *et al.* (1998).

(b) Pupillary isoresponse contour in cone contrast space

The sustained, delayed and larger pupillary response found with the isoluminant grating stimuli as compared with the isochromatic uniform stimuli suggests the involvement of the parvocellular pathway, in accordance with previous findings. The chromatic mechanism should respond preferentially to the isoluminant grating stimuli.

Figure 3. Normalized pupillary response amplitudes for (a) subject M. C. and (b) subject V. P. to the isoluminant grating stimuli (dashed line) and the isochromatic (solid line) uniform stimuli, thereby allowing their response latencies to be calculated. The amplitudes of the pupillary responses to the isochromatic and isoluminant stimuli were normalized with respect to the average amplitude and the traces overlaid such that differences in latency could be detected. The latency in the pupil responses ranged from 250 to 350 ms for all observers. The pupillary response evoked by the isoluminant grating is delayed by *ca.* 60 ms compared with that evoked by the isochromatic grating.

Isoresponse contours in cone contrast space were constructed in order to determine whether a linear chromatic mechanism was solely responsible for the pupillary responses evoked by the isoluminant grating stimuli. Therefore, the nature of an isoresponse contour plotted in

cone contrast space allows the pathway mechanism to be deduced. When the pupillary response is solely determined by the $|L-M|$ chromatic mechanism, the iso-response contour in cone contrast space should form parallel lines with a positive slope. Similarly, when the response is determined by the $|L+M|$ luminance mechanism it should form parallel lines with a negative slope. A poorly defined isoresponse contour is evident for the operation of nonlinear mechanisms.

The pupillary responses to four contrasts (0.04, 0.08, 0.12 and 0.16) along four vector directions (90, 117, 153 and 180°) were measured for observer J. W. in order to determine whether the pupillary response was approximately linear over this range. The response amplitude was recorded as the difference between the initial pupil diameter and the peak constriction. A linear relationship between the test contrast and the amplitude of the pupillary response was found to exist over the range examined (correlation coefficient $r > 0.90$ and $p < 0.05$ for all vector directions). Therefore, the isoresponse contrast (using a criterion of a 0.3 mm change in pupil size) for each vector direction was calculated from the pupillary response evoked by a test grating with a contrast of 0.16 for each of the four observers.

The isoresponse contour in cone contrast space was found to be linear and similar in gradient for each subject (see figure 4). The isoresponse contour for a chromatic grating was found to be linear ($r > 0.96$ for all observers) and positive in slope, indicating that the $|L-M|$ linear chromatic mechanism drives the pupillary response. The slope for the isoresponse contour reflects the weighted contribution of the long wavelength cone and medium wavelength cone contrasts. The slope for the four subjects ranged from 0.8 to 1.6 (average 1.1), which is close to the equally weighted difference of the long wavelength cone and medium wavelength cone contrasts in the red-green chromatic mechanism shown psychophysically by Chaparro *et al.* (1995).

4. DISCUSSION

(a) Comparison with previous studies

The sustained, delayed and larger pupillary response found when the responses to the isoluminant grating stimuli were compared with the isochromatic uniform stimuli suggests the involvement of the parvocellular pathway. The linear isoresponse contour in cone contrast space shows that the chromatic mechanism $|L-M|$ was solely responsible for the pupillary responses in the high contrast regions (*ca.* 20 times higher than the threshold for the isochromatic stimuli and *ca.* 32 times higher for the isoluminant stimuli) close to the isoluminant axis for this spatio-temporal frequency. In contrast, previous research by Kimura & Young (1995, 1996) showed that the contribution of the chromatic mechanism (i.e. the Sloan notch and chromatic cancellation) in the onset response could only be observed at low contrast close to the psychophysical threshold. Kimura & Young (1995, 1996) used a uniform flash field (30° diameter and 2.43 log troland) instead of a grating for showing the contribution of the chromatic mechanism. Although the difference in spatial frequency could influence the sensitivities of the luminance and chromatic mechanisms, we think

Figure 4. The pupillary isoresponse contour (for a change in amplitude of 0.3 mm) evoked by various colours of gratings modulated in cone contrast space. White circles represent the isoresponse contrasts for the 90, 117, 153 and 180° vector directions and the filled circles represent the 45° vector direction (isochromatic). The amplitude was measured as the difference between the initial pupil diameter and the peak constriction. The isoresponse contrast for each vector direction was calculated from the pupillary response amplitude and the stimulus contrast. As the grating stimuli were symmetrical modulations around the origin, both negative and positive contrasts are displayed in cone contrast space. r is Pearson's correlation coefficient.

that the most critical difference is in the colour of the test stimulus used. Kimura & Young (1995, 1996) used the luminance axis as their reference, whereas this experiment used the isoluminant axis as a reference.

Chaparro *et al.* (1995) considered whether stimuli around the Sloan notch corresponded to axes close to 45°

in cone contrast space (see fig. 13 in their paper), which allows some comparison of the results of this paper with those of Kimura & Young (1995, 1996). As shown in figure 4, because the sensitivity of the chromatic mechanism along the 45° axis is low, it is difficult to measure pupillary responses precisely around the Sloan notch and the luminance mechanism could contaminate the responses. It would therefore appear that the high contrast conditions of Kimura & Young's (1995, 1996) experiment could have led to pupillary responses that were contaminated by the luminance mechanism. In this study, for example, the data along the 45° axis for J. W. (figure 4a) are very close to the hypothetical chromatic contour (i.e. fitted parallel lines), thereby suggesting that this response was determined by both mechanisms since the sensitivity for both mechanisms is similar for this vector direction. On the other hand, this study used data points in the second and fourth quadrants of cone contrast space (see also figure 4) for estimating the slope of the contour. The sensitivity of the chromatic mechanism in these quadrants is much higher than that in the first and third quadrants, whilst the sensitivity of the luminance mechanism is much lower, thus avoiding contamination by the luminance mechanism.

(b) *Application in clinical and fundamental research*

The results of this study show that the pupillary iso-response contour is consistent with psychophysical measurement at high stimulus contrast, suggesting that the retinocortical pathway can be investigated using pupil measurement. Pupil measurements may therefore be useful for many applications in clinical and fundamental research. For instance, it may be feasible to detect the damage from glaucoma more reliably in a clinical setting using a pupillary response rather than a psychophysical measurement. In addition, the variability in psychophysical data from elderly patients or patients with systemic or ocular disease is often much higher than in the usual laboratory observer. Using higher contrast stimuli for isolating the chromatic mechanism will improve the signal-to-noise ratio of the pupil response and, thus, reduce response variability. Furthermore, in contrast to psychophysical measurements, the pupillary response can provide better indications of the temporal characteristics of the visual pathway, which may also find application in clinical assessment.

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