

A linear chromatic mechanism drives the pupillary response

S. Tsujimura, J. S. Wolffsohn and B. Gilmartin

Neurosciences Research Institute, Aston University, Aston Triangle, Birmingham, B4 7ET, UK

ABSTRACT

Previous studies have shown that a chromatic mechanism can drive pupil responses. The aim of this research was to clarify whether a linear or non-linear chromatic mechanism drives pupillary responses by using various colours of test stimuli defined in cone-contrast space. Pupil and accommodation responses evoked by these test stimuli were continuously and simultaneously measured objectively by photorefraction. The results with isochromatic and isoluminant stimuli showed that the accommodative level remained approximately constant ($<0.25D$ change in mean level) even when the concurrent pupillary responses was large ($\sim 0.30\text{mm}$). The pupillary response to an isoluminant grating was sustained, delayed (by $\sim 60\text{ms}$) and larger in amplitude than that for a 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 utilized and iso-response contours in cone-contrast space were obtained. The results showed that the iso-response 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 (L-cone) is subtracted from that of the Middle-wavelength cone (M-cone) and *vice versa*, drives pupillary responses.

INTRODUCTION

Although most visual information from the eye is transmitted directly to the visual cortex, some is routed to the pretectum, an area that controls the response characteristics of the pupils. The constriction and dilation of the pupil is evoked by changes in the ambient luminance. However, in addition to changes in retinal illuminance, the response of the pupil to visual stimuli can also be determined by factors such as cognition (Barbur, Wolf & Lennie, 1998) and changes in stimulus colour (Alpern & Campbell, 1962; Kohn & Clynes, 1969; Young & Alpern, 1980; Krastel, Alexandridis & Gertz, 1985; Barbur, Harlow & Sahraie, 1992; Young, Han & Wu, 1993;

Kimura & Young, 1995; Kimura & Young, 1996; Barbur, Wolf & Lennie, 1998; Gamlin, Zhang, Harlow & Barbur, 1998).

The two principal retino-cortical pathways, magno-cellular and parvo-cellular, mediate information on luminance and colour respectively (*e.g.* Derrington, Krouskopf & Lennie, 1984). In order to identify the pathways that contribute to the pupil response, several studies have examined how the pupil responds to specific changes in stimulus attributes: for example, the response to change in intensity as a function of wavelength, (*i.e.* action spectra, Alpern *et al.*, 1962; Krastel *et al.*, 1985; Kimura *et al.*, 1995) as a function of spatial structure (Ukai, 1985), and 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 pupil response.

In the case of the action spectra, if the magno-cellular pathway mediates the information transmitted to the pupil, the pupillary action spectra have a broadband property with a single peak in the middle-wavelength region. Conversely, if the parvo-cellular pathway mediates the information, 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-cone) is subtracted from that for the Middle-wavelength cone (M-cone) and *vice versa*, should have a prominent dip in sensitivity (*i.e.* a null or a minimum response) at around 570 nm (known as the Sloan notch). Some researchers have shown that the pupillary action spectrum has three prominent lobes, corresponding to the observations in psychophysics (Krastel *et al.*, 1985; Kimura *et al.*, 1995). In addition, Kimura *et al.* (1996) measured pupillary responses around Sloan notch and showed that responses evoked by a red flash could be neutralised by adding a green flash. These results suggest that a chromatic mechanism contributes to the pupillary response.

If the pupillary response were driven solely by a chromatic mechanism, the contribution of the chromatic mechanism could be observed independently of the stimulus contrast. However, Kimura *et al.*'s (1996) results showed that the contribution was observed only at very low contrast

near the psychophysical threshold. As contrast increases the pupillary action spectra 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 threshold. These results suggested that the dominant mechanism that drives pupillary response is not a chromatic mechanism at contrasts above threshold. Kimura *et al.* (1996) theorised that pupillary responses are modulated principally by the chromatic mechanism at low contrasts close to threshold, whereas above threshold levels, the pupillary response is likely to be determined by a compound mechanism with different action spectra (*e.g.* $|L-M|+|L+M|$). Some researchers (Young *et al.*, 1980; Barbur *et al.* 1998) showed a difference in latency of the pupillary response between isoluminant and luminance stimuli, suggesting that the balance between the different mechanisms was dependent on the visual stimuli.

The aim of this study is to clarify whether a linear (*i.e.* $|L-M|$) or non-linear (*i.e.* $|L-M|+|L+M|$) chromatic mechanism drives pupillary responses by using various colours of test stimuli defined in cone-contrast space. Of special note is that the test stimuli used to induce pupil responses were defined in cone-contrast space instead of wavelengths. This approach has two benefits. Firstly, as described in the method section, a pupillary iso-response contour in cone-contrast space was used to identify which mechanism contributes to the response. If the $|L-M|$ chromatic mechanism drives the pupillary response, the iso-response contour should form a straight line with a positive slope in cone-contrast space (*e.g.* Chaparro, Stromeyer, Chen & Kronauer, 1995). If the $|L+M|$ luminance mechanism drives the pupillary response, the contour should form a straight line with a negative slope (Tsujimura, Shioiri, Hirai & Yaguchi, 1999, 2000; Stromeyer, Chaparro, Tolia & Kronauer, 1997). However, if a non-linear mechanism drives the pupillary response, the contour would also be non-linear.

Secondly, as discussed later, test stimuli around the isoluminant axis are expected to produce much larger responses than around the Sloan notch for 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 Sloan notch and so the pupillary response is too small to specify the mechanism involved. Therefore, models

based on the Sloan notch have to rely on the assumption that the L-cone and the M-cone signals are linearly subtracted (Kimura *et al.*, 1996).

METHODS

Stimulus generation

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

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 which correspond to the excitation of the three kinds of cones in retina. The fundamentals were designed so that the total amount of excitation of Long-wavelength cones and Middle-wavelength cone is the same as Judd's modified photopic luminosity function $V(\lambda)$ (Smith and 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 was defined as: $C' = \Delta C / C_{Bg}$ (Eqn.1), where ΔC represents a difference in cone-excitation between the background and the test stimulus and C_{Bg} 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 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 S-cone excitation of the test stimulus was also kept constant (*i.e.* $\Delta S = 0$), allowing the data to be plotted in the L- and M-cone contrast space, such that the horizontal axis represents a stimulus modulating in L cone alone, and the vertical axis represents a stimulus modulating in M cone alone. Test stimuli consisted of a combination of L and M 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 having the same colour but different contrasts can be represented as vectors with the same direction but of different length. In Figure.1, the 45°-225° direction represents the isochromatic axis since the ratio of L- and M-cone excitation along this axis remains constant and is the same as that of background (*i.e.* $L_{Bg}/M_{Bg}=2.0$). In the first quadrant the L-cone modulation and the M-cone modulation 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 vector direction of 117°-297° (NB this is not the direction 135°-315° 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 L-and and M-cone modulations are out of phase in these quadrants.

The iso-response contour of the chromatic mechanism in cone-contrast space is expressed as $D=|aL'-bM'|$, where L' and M' are cone contrasts (Eqn.1), a and b represent the ratio of the L- and M-cone contrast 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 iso-response contour of the luminance mechanism is expressed as $D=|cL'+dM'|$, and describes lines with a negative slope.

Background stimuli

A yellow background with CIE 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 approximately 2.76 log photo td. 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 L cone contrast (*i.e.*, $r = L_{Bg}/(L_{Bg}+M_{Bg})$ in the cone excitation diagram proposed by MacLeod and Boynton, 1979) was 0.67 and the ratio of the L- and M-cone excitation 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. For a 570 nm yellow background field, Pokorny, Jin and Smith (1993) showed that 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 L- and M-cone inputs to the luminance mechanism were constant with respect to the change in spatial and temporal frequencies.

Test stimuli

The test stimulus was displayed in a circular region of 10° diameter at the centre of the screen for 2s. The pupillary and accommodative response was recorded for an additional 2s. Two spatial frequencies were used such that the test stimuli appeared uniform (0 c/deg) or as a grating (1.6 c/deg). Four test stimuli were used in the first experiment: an isochromatic 1.6 c/deg bright-yellow and dark-yellow grating (represented as **a-a'**); an isoluminant 1.6 c/deg orange and green grating (represented as **b-b'**); a bright yellow uniform stimulus (0 c/deg represented as **a**); and an isoluminant green uniform stimulus (0 c/deg represented as **b**; Figure 1). In the first experiment, a single contrast (0.16) was used and in the second experiment four contrasts (0.04, 0.08, 0.12, and 0.16) were used to investigate the linearity of the pupillary responses over this range. A contrast of 0.16 was chosen as it was over 20x greater than the psychophysical threshold measured initially.

Figure 1

Measurement of accommodation and Pupil Size

The pupil of the right eye was imaged using a video camera (Pulnix TM6) located 1 m from the subject, 15° temporal to the visual axis. An infra-red light source was mounted on the lower half of the video objective, which was masked. The infra-red light source produces a gradient of light intensity across the image of the pupil which is linearly correlated ($r = 0.95$ to 0.99) with accommodation and can be converted into dioptres following a simple calibration procedure (Schaeffel, Wilhelm & Zrenner, 1993). Changes in pupil size were found not to significantly affect, the intensity profile across the pupil 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) at a frequency of 50 Hz. The pupil was located using thresholding and edge detection techniques, allowing the pupil diameter to be analysed at a resolution of $<0.01\text{mm}$. The gradient of light intensity across the pupil was analysed, allowing the accommodative response to be quantified at a resolution of $<0.05\text{D}$.

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’, providing a strong closed-loop stimulus to maintain accommodation at a constant level. After an initial adaptation period of 3 minutes, a session of experimental trials began. The pupillary and accommodative response was continuously recorded from the observer’s right eye. Each of the test stimuli presentations were repeated and summed so that each trace represented an average of more than 30 recordings.

RESULTS

Pupil and accommodation responses evoked by isochromatic and isoluminant stimuli

The pupil and accommodation responses evoked by isochromatic and isoluminant stimuli for observer RC, whose data was typical of all 6 subjects, are shown in Figure 2. All test stimuli produced relatively large pupillary responses (on average $0.29 \pm 0.16\text{mm}$), but did not significantly affect the concurrent accommodative level (Difference = 0.00 ± 0.06 , $p=0.99$). The pupillary response evoked by the isoluminant grating (Figure 2, upper right panel) was slow to re-dilate (*i.e.* a sustained temporal property), suggesting involvement of the parvo-cellular pathway noted in previous studies (*e.g.* Gouras, 1968; Young & Alpern, 1980; Anderson, S.J. & Burr, 1985; Kimura *et al.*, 1995). The isoluminant green uniform stimulus (Figure 2, lower right panel) evoked a large, transient response with a secondary dip. This finding is consistent with

results reported and have been attributed to afterimage cortical mechanisms (Barbur *et al.*, 1998, 1999) and to OFF responses (Kimura *et al.*, 1995).

Figure 2

The finding for all subjects that pupillary responses to isoluminant stimuli were consistently larger than those evoked by isochromatic stimuli runs counter to the widely accepted view that the pupillary response is driven predominantly by the luminance mechanism. It would appear that pupillary responses can be driven separately 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 c/deg) 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 base-line) were shown to have two characteristics: first, time courses were independent of contrast level after normalisation; secondly, time courses were equivalent for within-class variations in stimulus level (*e.g.* contrast) but different for between-class variation in stimulus level (*e.g.* uniform colour field and luminance gratings). The amplitude of the pupillary response to isoluminant grating and isochromatic uniform stimuli were normalised with respect to the average amplitude and the traces overlaid such that differences in latency could be detected. Figure 3 shows onset latencies for observers MC and VP. The latencies for the isoluminant grating were significantly longer (differences for each of the subjects: -28.2, 65.5, 65.6, 79.8, 88.1 and 98.4ms; $p < 0.05$), on average by 62ms, than those found for the isochromatic uniform stimulus and were similar to those reported by Barbur *et al.* (1998).

Figure 3

Pupillary iso-response contour in cone-contrast space

The sustained, delayed and larger pupillary response found with isoluminant gratings compared to isochromatic uniform stimuli suggests the involvement of the parvo-cellular pathway, in accordance with previous findings. The chromatic mechanism should respond preferentially to the isoluminant grating. To determine whether a linear chromatic mechanism was solely responsible for the pupillary responses evoked by the isoluminant grating, iso-response contours in cone-contrast space were determined. Therefore, the nature of an iso-response 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 iso-response contour is evident for the operation of non-linear 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 JW 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 $r > 0.90$, $P < 0.05$ for all vector directions). Therefore, for each of the four observers the iso-response 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.

The iso-response contour for each subject in cone-contrast space was found to be linear and similar in gradient (see Figure 4). The iso-response 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 iso-response contour reflects the weighted contribution of the L- and M-cone contrasts. The slope for the 4 subjects

ranged from 0.8 to 1.6 (average 1.1), which is close to the equally-weighted difference of L- and M-cone contrast in the red-green chromatic mechanism shown psychophysically by Chaparro *et al.* (1995).

Figure 4

DISCUSSION

Comparison with previous studies

The sustained, delayed and larger pupillary response found when responses to isoluminant gratings were compared to isochromatic uniform stimuli suggests the involvement of the parvocellular pathway. The linear iso-response contour in cone contrast space shows the chromatic mechanism $|L-M|$ was solely responsible for the pupillary responses in the high contrast regions (~ 20 times higher than threshold for the isochromatic stimuli and ~ 32 times higher for the isoluminant stimuli) close to the isoluminant axis for this spatio-temporal frequency. In contrast, previous researches by Kimura *et al.* (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 *et al.* (1995, 1996) used uniform flash field (30-deg diameter, 2.43 log td) instead of grating to show the contribution of chromatic mechanism. Although the difference in spatial frequency could influence sensitivities of luminance and chromatic mechanisms we think most critical difference is the difference in colour of the test stimulus used. Kimura *et al.* 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 Figure 13 in their paper) which allows some comparison of the results of this paper with those of Kimura *et al.* As shown in Figure 4, since 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 *et al.*'s experiment could have led to pupillary responses that were contaminated by the luminance mechanism. In this study, for example, data along the 45° axis for JW (left panel) are very close

to the hypothetical chromatic contour (*i.e.* fitted parallel lines), 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) to estimate the slope of the contour. In these quadrants, the sensitivity of the chromatic mechanism 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.

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 retino-cortical pathway can be investigated using pupil measurement. Pupil measurements may therefore be useful for many applications in clinical and fundamental research. For instance, in a clinical setting, it may be feasible to detect the damage from glaucoma more reliably using a pupillary response than using a psychophysical measurement. In addition, the variability of psychophysical data from elderly patients or patients with systemic or ocular disease is often much higher than the usually laboratory observer. Using higher contrast stimuli to isolate 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.

ACKNOWLEDGMENTS

Sei-ichi Tsujimura was supported by The Leverhulme Trust, Overseas Fellowship Scheme, UK. We would like to thank John L. Barbur, City University, London, for his comments on the original data and Harry Wyatt, SUNY College of Optometry and Eiji Kimura, Osaka Prefecture University, for their comments on the manuscript.

Running Heading: Pupil response to colour

Short title for page heading: A linear chromatic mechanism drives the pupillary response

Address for Correspondence:

Dr Sei-ichi Tsujimura

Postdoctoral Research Fellow

Department of Clinical Sciences

SUNY College of Optometry, 7th floor

33 West 42nd Street

New York NY 10036

email: stsujimura@sunyopt.edu

phone: 212.780.5939

fax: 212.780.5207

Summary: 195 words

Main body 3500 words

Figure captions: 362 words

Reference: 587 words

Number of figures: 4

FIGURE CAPTIONS

Figure 1.

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

Figure 2. Pupil and accommodation responses for observer RC. The right column represents isoluminant test stimuli and the left column represents isochromatic stimuli. The upper row represents grating stimuli (1.6 c/deg) and the lower row uniform stimuli (0.0 c/deg). Each trace represents the average of more than 30 recordings. The onset and offset of the test stimulus are shown by the grey box on the time scale axis.

Figure 3. Normalised pupillary response amplitudes for subjects MC and VP to isoluminant grating (dashed line) and isochromatic (solid line) uniform stimuli, allowing response latencies to be calculated. The amplitudes of the pupillary response to isochromatic and isoluminant stimuli were normalised with respect to the average amplitude and the traces overlayed such that differences in latency could be detected. The latency in pupil response ranged from 250 to 350 ms for all observers. The pupillary response evoked by the isoluminant grating is delayed by approximately 60 ms compared to that evoked by the isochromatic grating.

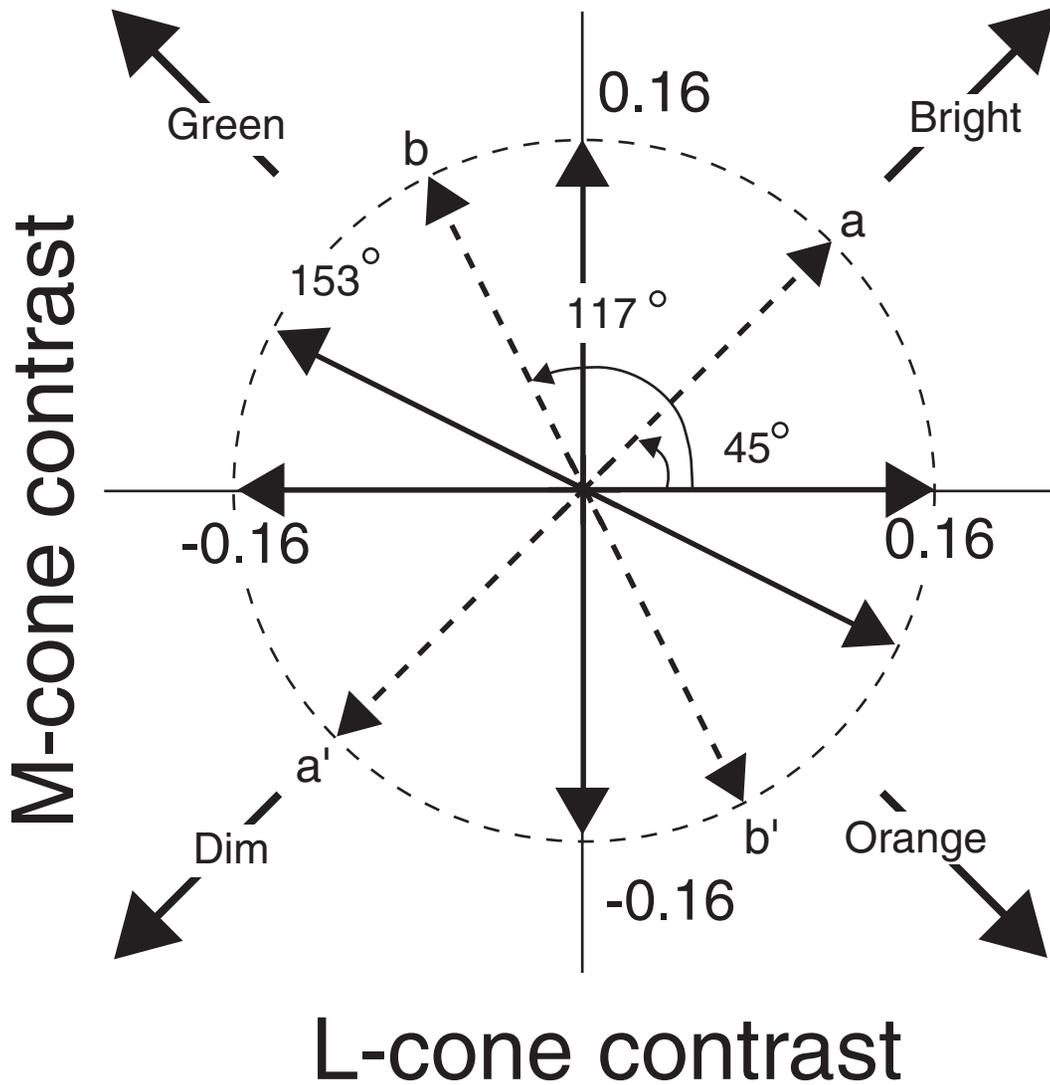
Figure 4. The pupillary iso-response contour (for a change in amplitude of 0.3mm) evoked by various colours of gratings modulated in cone-contrast space. White circles represent the iso-response contrasts for 90°, 117°, 153° and 180° vector directions and the filled circle represents

the 45° vector direction (isochromatic). The amplitude was measured as the difference between the initial pupil diameter and the peak constriction. The iso-response contrast for each vector direction was calculated from the pupillary response amplitude and the stimulus contrast. Since grating stimuli were symmetrical modulations around the origin, both negative and positive contrast are displayed in cone-contrast space. r = Pearson's Correlation Coefficient.

REFERENCES

- Alpern M. & Campbell F. W. 1962 The spectral sensitivity of the consensual light reflex. *J. Physiol.* **164**, 478-507.
- Anderson, S.J. & Burr, D.C. 1985 Spatial and temporal selectivity of the human motion detection system. *Vision Res.* **25**, 1147-1154.
- Barbur, J.L., Harlow, A.J. & Sahraie, A. 1992 Pupillary responses to stimulus structure, colour and movement. *Ophthal. Physiol. Opt.* **12**, 137-141.
- Barbur, J. L., Weiskrantz, L. & Harlow, A.J. 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.
- Barbur, J.L., Wolf, J. & Lennie, P. 1998 Visual processing levels revealed by response latencies to changes in different visual attributes. *Proc. R. Soc. Lond. B* **265**, 2321-2325.
- Chaparro, A., Stromeyer III, C.F., Chen, G. & Kronauer, R. E. 1995 Human cones appear to adapt at low light levels: Measurements on the red-green detection mechanism. *Vision Res.* **35**, 3103-3118.
- Gamlin, P. D. R., Zhang, H., Harlow, A. & Barbur, J.L. 1998 Pupil responses to stimulus color, structure and light flux increments in the rhesus monkey. *Vision Res.* **38**, 3353-3358.
- Gouras, P. 1968 Identification of cone mechanisms in monkey ganglion cells. *J. Physiol.* **199**, 533-547.
- Kimura, E. & Young, R. S. L. 1995 Nature of the pupillary responses evoked by chromatic flashes on a white background. *Vision Res.* **135**, 897-906.
- Kimura, E. & Young, R. S. L. 1996 A chromatic-cancellation property of human pupillary responses. *Vision Res.* **36**, 1543-1550.
- Kohn, M. & Clynes, M. 1969 Color dynamics of the pupil. *Annals of the New York Academy of Science* **15**, 931-950.
- Krastel, H. Alexandridis, E. & Gertz, J. 1985 Pupil increment thresholds are influenced by color opponent mechanisms. *Ophthalmologica* **191**, 35-38.
- MacLeod, D.I.A. & Boynton, R. M. 1979 Chromaticity diagram showing cone excitation by stimuli of equal luminance. *J. Opt. Soc. Am.* **8**, 1183-1186.

- Schaeffel, F., Wilhelm, H. & Zrenner, E. 1993 Inter-individual variability in the dynamics of natural accommodation in humans: relation to age and refractive errors. *J. Physiol.* **461**, 301-320.
- Smith, V.C. & Pokorny, J. 1975 Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Res.* **15**, 161-171.
- Stromeyer III, C. F., Chaparro, A., Toliás, A. S. & Kronauer, R. E. 1997 Colour adaptation modifies the long-wave versus middle-wave cone weights and temporal phases in human luminance (but not red-green) mechanism. *J. Physiol.* **499**, 227-254.
- Stromeyer III, C. F., Kronauer, R. E., Ryu, A., Chaparro, A. & Eskew Jr, R. T. 1995 Contributions of human long-wave and middle-wave cones to motion detection. *J. Physiol.* **485**, 221-243.
- Tsujimura, S., Shioiri, S., Hirai, Y. & Yaguchi, H. 1999 Selective cone suppression by the L-M and M-L cone-opponent mechanisms in the luminance pathway. *J. Opt. Soc. Am. A.* **16**, 1217-1228.
- Tsujimura, S., Shioiri, S., Hirai, Y. & Yaguchi, H. 2000 A technique to investigate the temporal phase shift between L- and M-cone inputs to the luminance mechanism. *J. Opt. Soc. Am. A.* **17**, 846-857.
- Ukai, K. 1985 Spatial pattern as a stimulus to the pupillary system. *J. Opt. Soc. Am. A.* **2**, 1094-1100.
- Pokorny, J., Jin, Q. & Smith, V. C. 1993 Spectral-luminosity functions, scalar linearity, and chromatic adaptation. *J. Opt. Soc. Am. A* **10**, 1304-1313.
- Young, R. S. L. & Alpern, M. 1980 Pupil responses to foveal exchange of monochromatic lights. *J. Opt. Soc. Am.* **70**, 697-706.
- Young, R. S. L. & Teller, D. Y. 1991 Determination of lights that are isoluminant for both scotopic and photopic vision. *J. Opt. Soc. Am. A* **8**, 2048-2052.
- Young, R. S. L., Han, B. & Wu, P. 1993 Transient and sustained components of the pupillary responses evoked by luminance and color. *Vision Res.* **33**, 437-446.



Exp.1: Dashed lines

a-a') Isochromatic grating

L-cone signal

+

M-cone signal

b-b') Isoluminant grating

L-cone signal

+

M-cone signal

a) Isochromatic uniform

L-cone signal

+

M-cone signal

b) Isoluminant uniform (green)

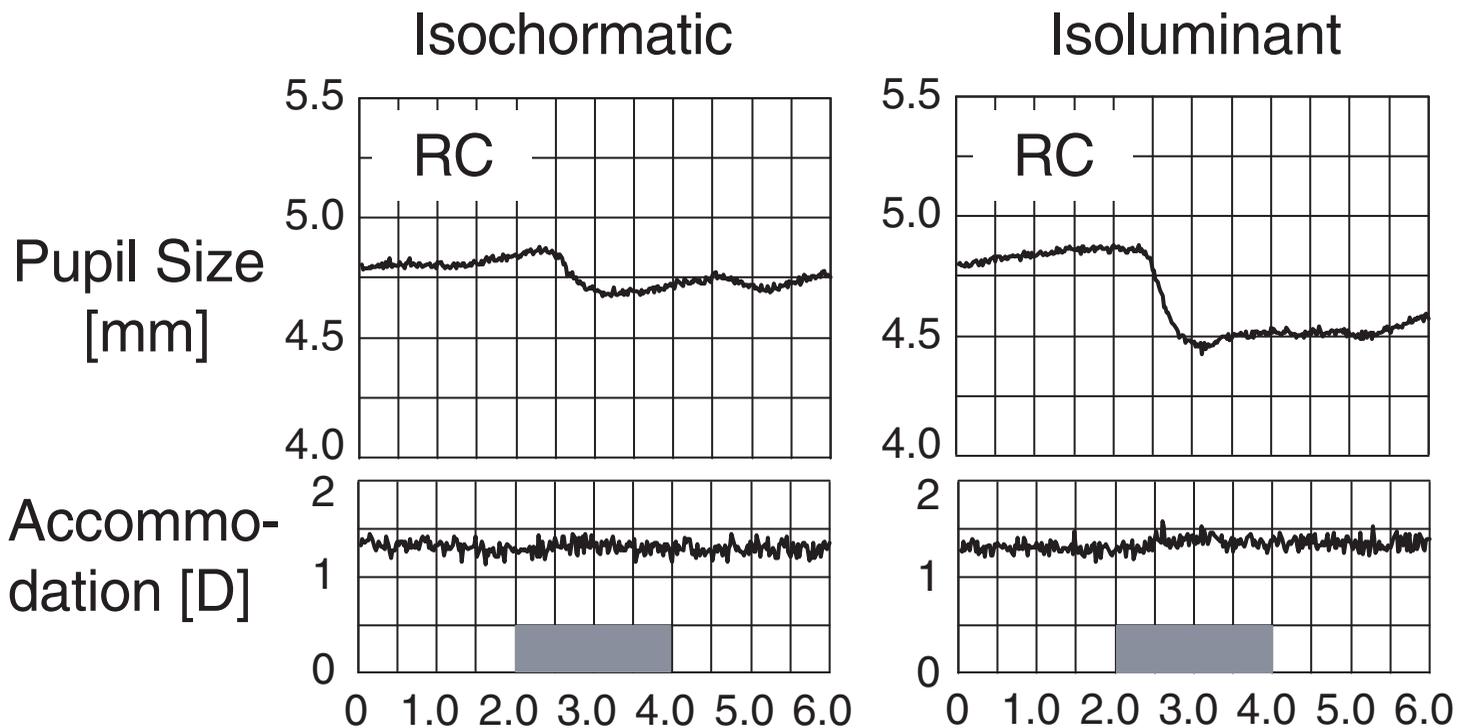
L-cone signal

+

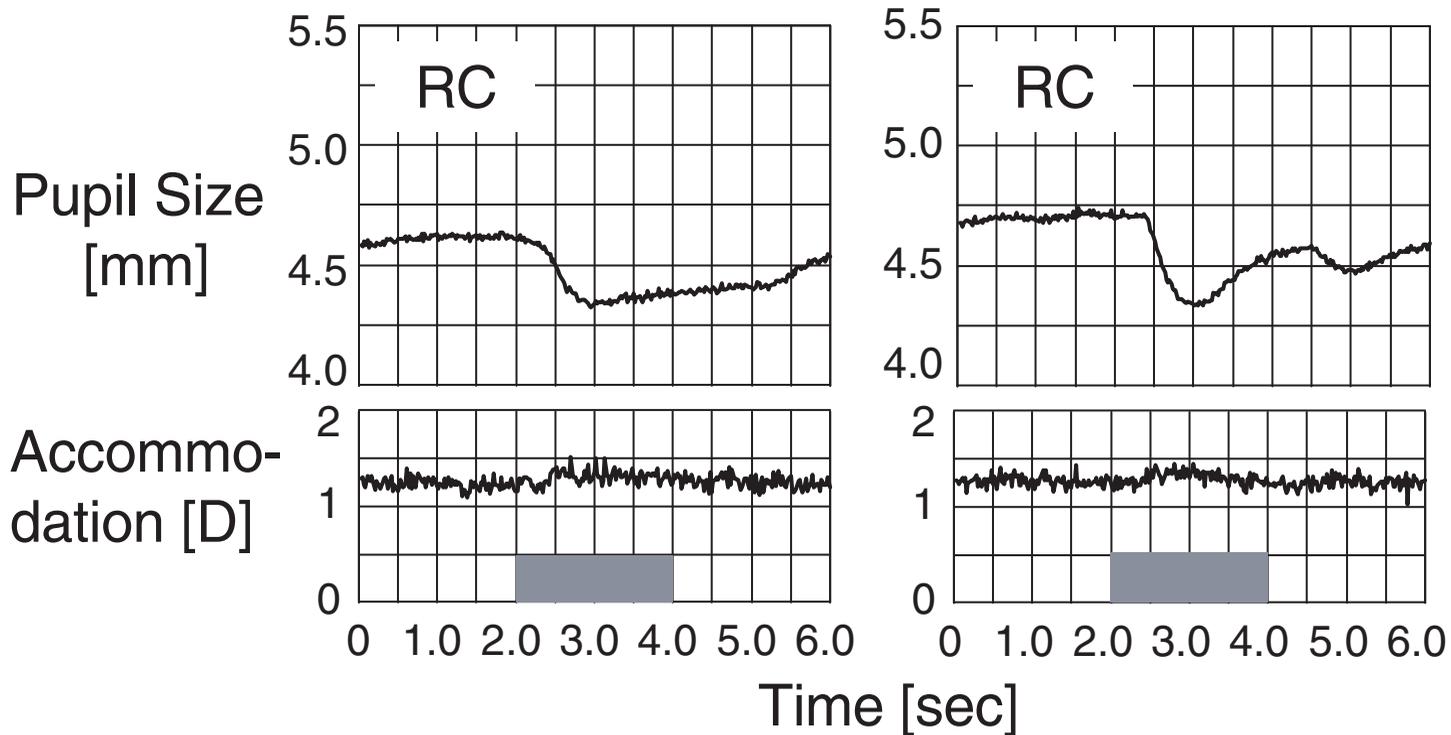
M-cone signal

Exp.2: Solid lines

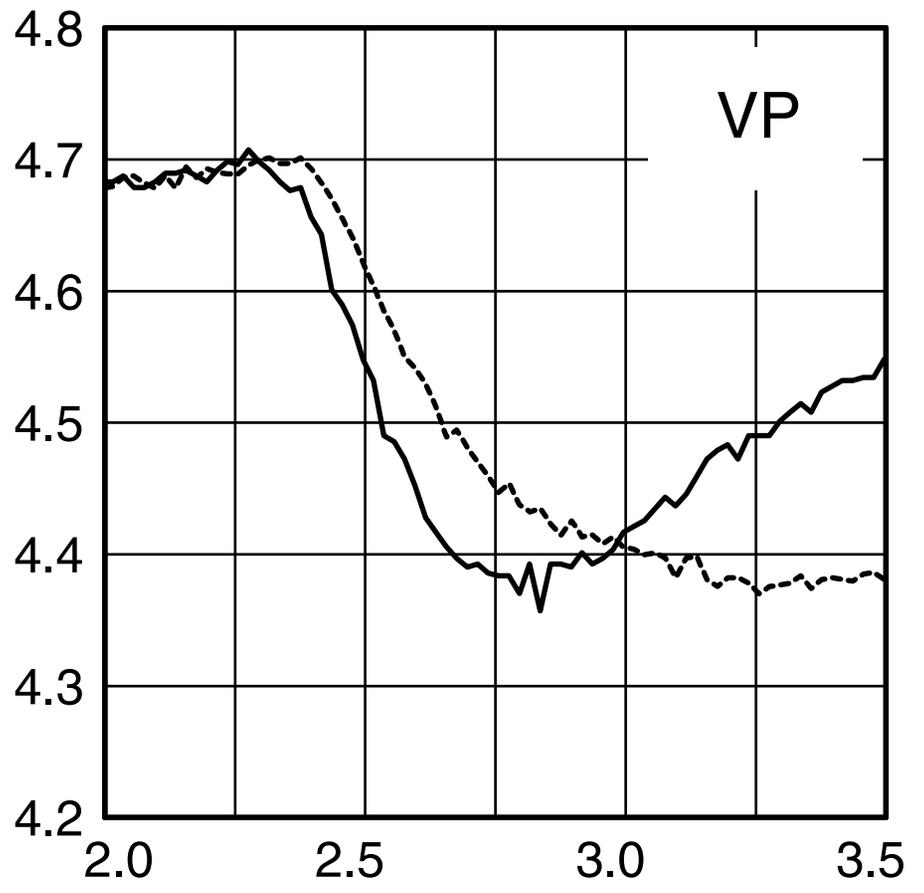
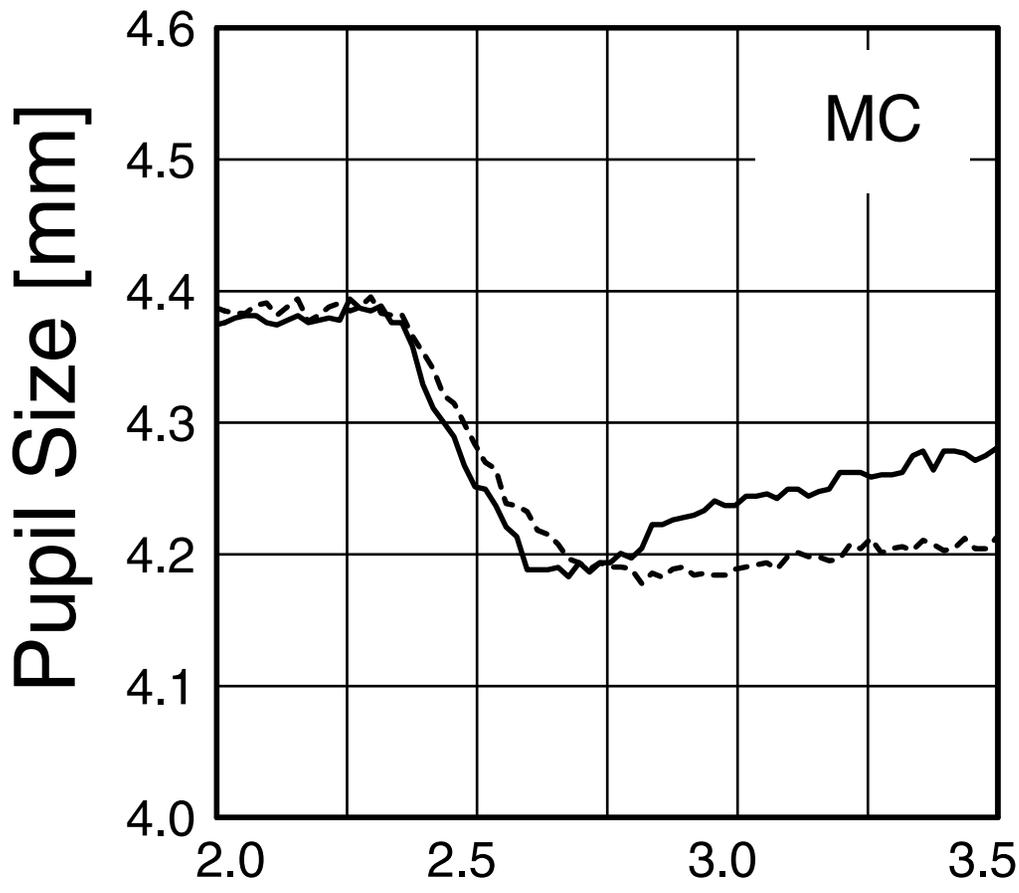
Grating



Flash



---- Isoluminant grating
— Isochromatic flash



Time [sec]

