Vision Research 159 (2019) 42–47

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

# Evidence for a central component in adaptation to chromatic light

Hitomi Shimakura[a,*], Katsuaki Sakata[b]

[a] *Shiseido Global Innovation Centre, 1-2-11, Takashima, Nishi-ku, Yokohama, Kanagawa 220-0011, Japan*
[b] *Joshibi University of Art and Design, 1900, Asamizodai, Minami-ku, Sagamihara, Kanagawa 252-8538, Japan*

ARTICLE INFO

Number of reviewers: 1

*Keywords:*
After-effects
Binocular summation
Color
Chromatic adaptation
Contrast adaptation

ABSTRACT

Adaptation to environmental light allows our visual system to compensate for dynamic changes in the visual environment for avoiding everyday hazards (e.g., misreading traffic lights) and for accurate reaching. We investigated the hypothesis that adaptation to coloured light is achieved not only via photoreceptors in the retina and monocular contrast adaptation, but also by a binocular process that may occur at the level of the cerebral cortex. In the present study, to determine the role of higher-order cortical binocular processes in adaptation to coloured light, participants were adapted to chromatic light such that the duration of adaptation during monocular processing differed from that during binocular processing. A dichoptic device was used to adapt each eye independently. The extent of after-effects, measured as the distance between the neutral points before and after adaptation to coloured light, depended on the duration of adaptation not only at the monocular level but also at a higher cortical level downstream from binocular fusion. Thus, contrast adaptation to coloured light occurs on at least two levels; it is a result of monocular processes at one level and binocular processes at the other, and each type of process exhibits different temporal characteristics. The results of this study suggest a significant cortical role in adaptation to changes in lighting conditions or the optical environment, including the effects of age on the eye, and the necessity of further investigation to clarify the functional connection between chromatic adaptation by photoreceptors and chromatic adaptation by cortical systems.

## 1. Introduction

Although vision, based on visible light, is our most reliable sense, our environmental conditions demand a very broad range of adaptations to daily light changes. Although most previous studies have investigated adaptation to short-term exposure to coloured light (i.e., a few seconds), primarily with respect to retinal mechanisms, some research groups have examined long-term adaptation (i.e., $\geq 1$ h) (Belmore & Shevell, 2011; Neitz, Carroll, Yamauchi, Neitz, & Williams, 2002). Two mechanisms for adaptation to chromatic light have been proposed (Webster & Wilson, 2000; Webster, 1996). First, adaptation to coloured light—namely light adaptation and chromatic adaptation, explained by a selective decrease in sensitivity in the three types of retinal photoreceptors—has been attributed to neural gain control in the three types of retinal cones. This type of adaptation adjusts the sensitivities of photoreceptors to the centroid of intensities and chromaticities of light to maintain them within the most sensitive range. Several studies have investigated this type of adaptation (Hunt, 1950; Nayatani, Hashimoto, Takahama, & Sobagaki, 1987) in various contexts such as aging (Werner, Bayer, Schwarz, Zrenner, & Paulus, 2010), temporal saliency in the mechanisms underlying adaptation (Barrionuevo et al., 2018), and the relationship between lightness and signals from different photoreceptors (Huchzermeyer et al., 2018).

The other type of adaptation is known as contrast adaptation, which adjusts the latitude of sensitivity depending on the distribution of intensities and chromaticities of light in the field of vision. This type of adaptation tunes colour appearance by changing the contrast along the larger distribution of light, so that the dynamic range of our visual sensitivities can cover various distributions of light in our visual environment. Research has indicated that performance during visual search tasks depends on both contrast and chromatic adaptation to the background (McDermott, Malkoc, Mulligan, & Webster, 2010). Previous studies have demonstrated that chromatic contrast adaptation begins after the photoreceptor stage in the retina, while light and chromatic adaptation begins at the retinal photoreceptors (Howlett, Smith, & Kamermans, 2017). Many studies have revealed post-photoreceptor loci for contrast adaptation not only to colour properties, but also to many sensory aspects (Cooke, King, Willmore, & Schnupp, 2018; Keller et al., 2017; King, Lowe, & Crowder, 2015; Liu & Gollisch, 2015; Vergeer, Mesik, Baek, Wilmerding, & Engel, 2018; Zhuang & Shevell, 2015). Researchers have suggested that the after-effects of contrast adaptation measured in the adapted eye arise due to the involvement of

---

[*] Corresponding author.
*E-mail addresses:* hitomi.shimakura@to.shiseido.co.jp (H. Shimakura), sakata00031@venus.joshibi.jp (K. Sakata).

https://doi.org/10.1016/j.visres.2019.02.015
Received 30 June 2018; Received in revised form 1 February 2019; Accepted 27 February 2019

both monocular and binocular neurons, while those measured in the non-adapted eye are determined only by binocular neurons (Blake, Overton, & Lema, 1981). In this context, the term 'monocular neurons' refers not only to photoreceptors, but also to all levels prior to binocular fusion in our visual system. The three-cone mechanism in the retina, which is thought to be a factor in chromatic adaptation, constitutes one part of this monocular process. However, post-photoreceptor processes, which implement contrast effects, are thought to also reside at the cortical level, and are thus considered to be involved in the binocular process (Blake & Overton, 1979; O'Shea & Crassini, 1981). Therefore, it is reasonable to assume that the term 'binocular process' in this context refers to a higher-order process downstream from the striate (primary visual) cortex. However, previous studies that explored whether the retinal processes results in contrast adaptation shows little evidence of the binocular process contributing to chromatic adaptation.

In the present study, we aimed to explore the effects of long-term adaptation. We used psychophysical methods to investigate whether a 'binocular process' is involved in adaptation to chromatic light. We regarded the process of integrating information from the eyes, which is the same regardless of the eye to which the light is presented, as a binocular process, the function of which does not depend on either the right or the left eye in terms of the chromatic after-effects. As previous studies have demonstrated that chromatic adaptation is cumulative (Belmore & Shevell, 2011; Dong, Engel, & Bao, 2014), we measured the build-up of after-effects in the monocular and binocular processes during adaptation to chromatic light by presenting the light stimuli to each eye independently.

## 2. Materials and methods

### 2.1. Participants

The experiment included 11 female volunteers (mean age 22.6 years, range 19–34), in whom normality of colour vision was assessed using Ishihara plates. The experiment adhered to the tenets of the Declaration of Helsinki and was performed after providing each participant with a thorough explanation of the study protocol, the underlying principle, and other information, including the methods of colour vision testing to be employed. Each participant provided written informed consent prior to participation in the study. The study protocol was approved by the ethics committee at Joshibi University of Art and Design.

### 2.2. Apparatus

Stimuli were presented on a CRT monitor (FlexScan T561, Eizo Nanao Corporation, Hakusan, Japan; 1024 × 768 pixels; 120 Hz; visual angle, 23.5° × 31°) driven by a personal computer. Each participant was seated approximately 57 cm from the monitor with her head stabilised by a chin rest. A dichoptic device and a 2-mm diameter artificial pupil were used. The entire experiment was performed in a dark room.

### 2.3. Stimuli

An adapting light with CIE chromaticity coordinates of $x = 0.291$ and $y = 0.606$, a luminance of 77.8 cd/m$^2$, and a size of 23.5° × 15.5° was presented on the CRT monitor. To measure the strength of after-effects, a circular test stimulus with a visual angle of 2° was presented on the centre of the same CRT screen, its colour varying in 81 steps from red to green. This test stimulus was previously adjusted using minimum flicker photometry to be isoluminant for each study participant. Fig. 1 shows the range of the chromaticity coordinates of the test stimulus used to measure the after-effects of adaptation. Minimum flicker photometry was performed for each participant to adjust the luminance the red (△) and green (□) colours at both ends of the test stimulus range to that of the yellow (○) colour, which was chosen to have approximately the same saturation as the red and green stimuli to avoid the influence of saturation.

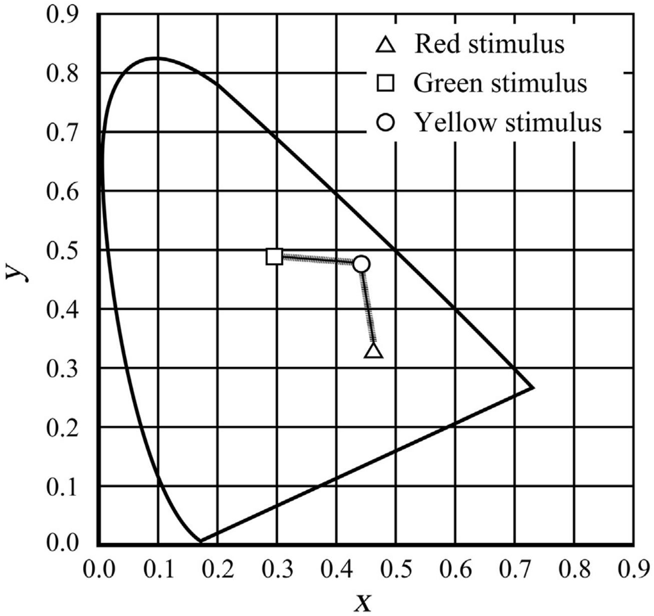

**Fig. 1.** Test stimuli for the adjustment method are shown. The path shown on the CIE *x*-*y* chromaticity diagram indicates the adjustment range for the test stimuli, which varied through 81 steps. Minimum flicker photometry was performed for each study participant. The red (Δ) and green (□) stimuli, which occupied opposite ends of the test-stimulus range, were adjusted to a luminance equivalent to that of the yellow stimulus (○).

### 2.4. Procedure

The pre-experiment appearances of the colour used as a reference point to measure the strength of after-effects of adaptation to chromatic light were recorded for each study participant. After 15 min of dark adaptation, each participant was asked to adjust a test stimulus to a colour with no perceptible redness or greenness via an artificial pupil that had a diameter of 2 mm. The trials were repeated ten times, and the average of the ten measurements was recorded as the result.

Two types of adaptation conditions were established: anti-phase adaptation, in which the phase of the stimulus presentations varied for each eye, and in-phase adaptation, in which the phases of the stimuli provided to the left and right eye corresponded (Fig. 2). Following 15 min of dark adaptation (b) to measure the neutral points, the dominant eye of the anti-phase condition was exposed to the chromatic adaptation stimulus for 10 min (a), following which the non-dominant eye was exposed for 10 min. These sequences were then repeated, and the appearances of the non-red and non-green points were measured for the dominant eye by adjusting the test stimuli (d) through the observer's dominant eye divided by the dichoptic shield (e) after a dark inter-stimulus interval (c). Under the in-phase condition, both eyes were exposed to the chromatic adaptation light simultaneously for 10 min, followed by dark adaptation for 10 min. These sequences were also repeated, and the appearance of the corresponding neutral point was measured in the observer's dominant eye. The durations of adaptation were identical for each eye and for each condition, and the duration between extinction of the last adaptation stimulus and the start of measurement was also identical in both adaptation conditions. The size of the test stimulus, luminance, and duration of presentation for the monocular process were identical under both conditions.

Three participants (α, β, γ) were assigned to the in-phase condition, three (δ, ε, ζ) were assigned to the anti-phase adaptation condition (between-subjects design), and another five (η, θ, ι, κ, λ) were assigned

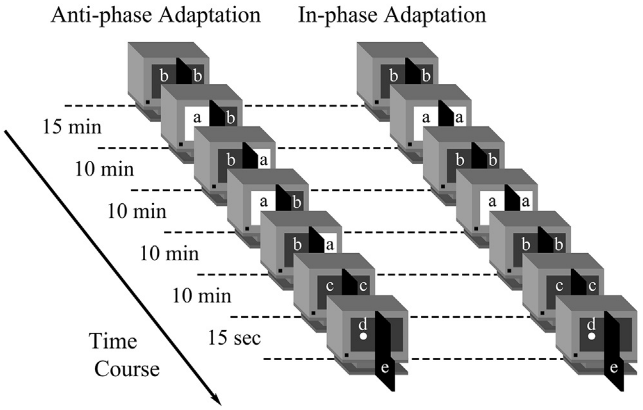

**Fig. 2.** Time course of stimulus presentation under the two adaptation conditions. The figure shows an example of the experimental paradigm when measuring after-effects for the left eye. The symbols in the diagram represent (a) chromatic adapting light, (b) no stimulus, (c) the inter-stimulus interval, (d) the test stimulus, and (e) a dichoptic device. The stimuli were presented with right and left reversed when the right eye was dominant.

to both conditions (within-subject design). In the last case, each participant was exposed to the in-phase adaptation condition or anti-phase condition and then exposed to the alternative condition after an interval of at least 1 week.

One previous report suggested the presence of large individual differences in the time required to recover from adaptation to chromatic light (Eisner & Enoch, 1982). Therefore, the strength of the after-effects was compared within the same participant to determine the accumulation of after-effects attributable to adaptation. Prior to the second measurement, the appearance of the colour was re-evaluated to confirm that the effects of the previous adaptation had disappeared. This minimised the possibility that the strength of the observed after-effects depended on individual differences, a possibility pointed out in a previous study (Fairchild & Reniff, 1995).

The strength of after-effects was assumed to be the distance between the non-red and non-green points before and after adaptation to chromatic light based on the MacLeod-Boynton chromaticity coordinates (MacLeod & Boynton, 1979), which were originally calculated using cone sensitivities (Stockman & Sharpe, 2000).

### 2.5. Statistical analysis

The effects of adaptation were taken as the aftereffect sizes, expressed as distances in the MacLeod-Boynton colour space, for purposes of comparison. These comparisons were analysed using a *t*-test after a Levene's test to confirm equality of variances. These analyses were calculated using a VBA software in a Microsoft Excel environment.

## 3. Results

The average loci of the non-red and non-green appearances for each of the three participants of the between-subjects group (Fig. 3A) and within-subject group (Fig. 3B) after adaptation to chromatic light (shown as discs for the anti-phase and diamonds for the in-phase conditions) were compared with those before chromatic adaptation. Under both conditions, the neutral points moved from the loci before chromatic adaptation (filled symbols) to the loci after chromatic adaptation (empty symbols) (i.e., chromatic after-effects). Moreover, the distance of the transition under the anti-phase condition was greater than that under the in-phase condition (i.e., the after-effects resulting from anti-phase adaptation were more intense than were those resulting from in-phase adaptation).

Regardless of the adaptation condition, the non-red, non-green point after adaptation to chromatic light approached that of the adapting light in all three participants under the anti-phase condition, thereby confirming adaptation. However, there was a little difference under the in-phase adaptation condition (i.e., weak adaptation).

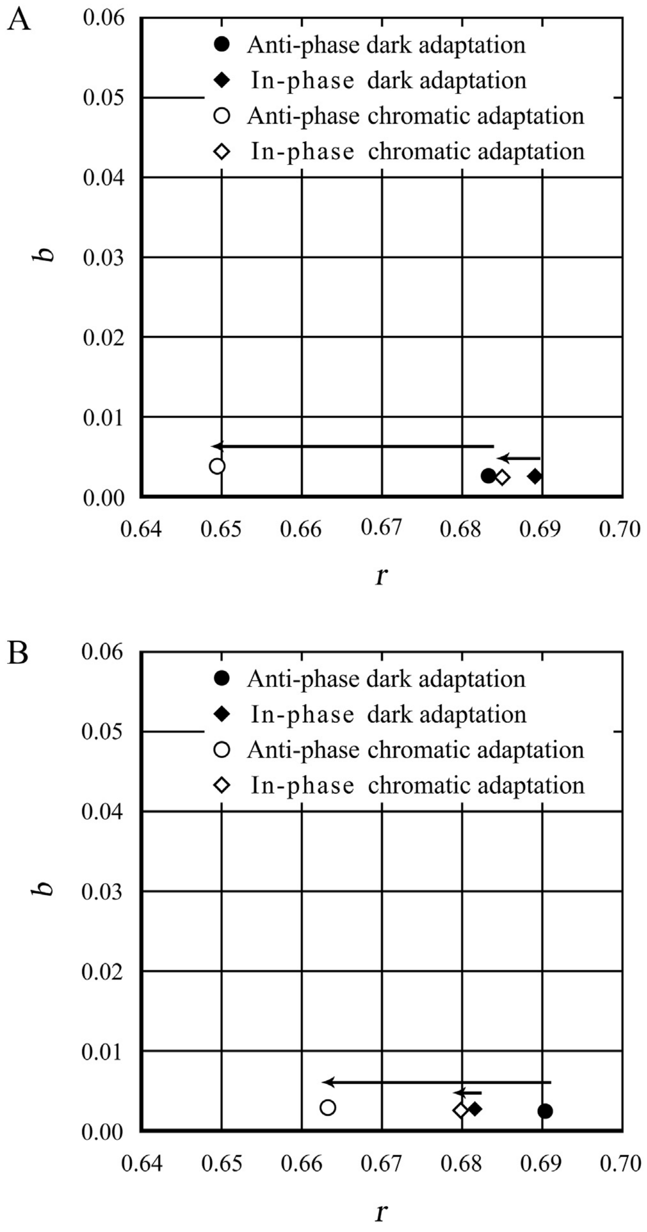

**Fig. 3.** Shift of non-red and non-green colour appearance before and after chromatic adaptation. Changes in colour appearance before (filled symbols) and after (empty symbols) green chromatic adaptation. The results under the anti-phase condition are indicated by discs, while those under the in-phase condition are indicated by diamonds. Figure A shows the average results for the between-subjects condition in which three individuals participated in the in-phase condition and the other three individuals participated in the anti-phase condition. Figure B shows the results for the within-subject comparisons and reveals the stability of the difference between the anti-phase condition and the in-phase condition.

Fig. 4A and B show a comparison of the distance between the neutral points before and after chromatic adaptation under the anti-phase (■) and in-phase (□) conditions. Fig. 4A and B show the results of the between-subjects and within-subject comparisons, respectively. In both figures, the abscissa indicates the participant, while the ordinate indicates the distance between the neutral points before and after chromatic adaptation. The after-effects of chromatic adaptation under the anti-phase condition were significantly more pronounced than those

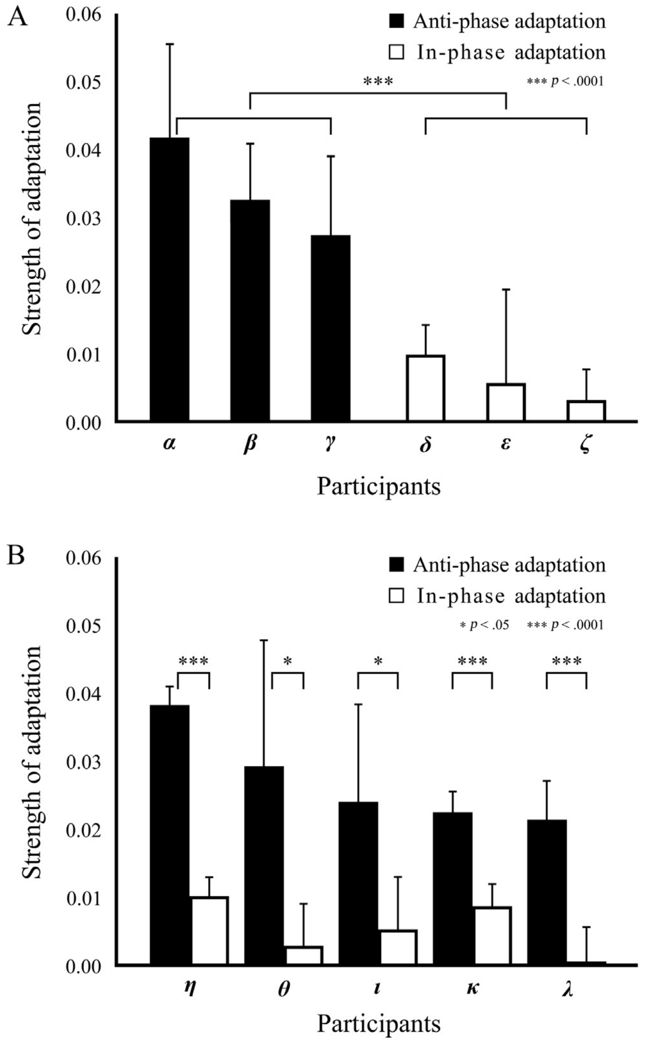

**Fig. 4.** Colour difference in the adjusted value before and after chromatic adaptation to green light. The colour difference in the MacLeod-Boynton colour space indicates the strength of adaptation. The abscissa indicates participants for each type of adaptation condition, the ordinate indicates the strength of after-effects, filled bars indicate the results of anti-phase adaptation, and empty bars indicate the results of in-phase adaptation. The strength of after-effects was greater under anti-phase adaptation conditions than under in-phase adaptation conditions for all participants, regardless of whether the comparison was between subjects or within subjects. The error bars represent ± 1 standard deviation.

under the in-phase condition, despite large inter-individual differences in the strength of the after-effects. Since Levene's test for variance revealed statistically significant differences in standard deviation ($W = 5.36, p = .024$) for the between-subject groups, an independent $t$-test was used, revealing a significant difference between the two adapting groups ($t\ [52.77] = 8.17, p < .0001$). For the within-subject group, a paired sample $t$-test or an independent sample $t$-test was performed depending on the equality of variances for each participant after Levene's test. This analysis also revealed differences between the two adapting conditions ($W = 0.01, p = .915, t\ [11] = 122.65, p < .0001$ for observer η; $W = 11.69, p = .003, t\ [10.89] = 3.08, p = .011$ for observer θ; $W = 5.05, p = .035, t\ [16.90] = 2.28, p = .036$ for observer ι; $W = 0.15, p = .701, t\ [11] = 6.33p < .0001$ for observer κ; and $W = 1.10, p = .308, t\ [18] = 4.59, p < .0001$ for observer λ).

## 4. Discussion

Although numerous studies have investigated binocular colour interactions (e.g. Hecht, 1928), dichoptic colour mixing remains a controversial issue (Hovis, 1989; Wade, 2018). The results of the present study verify the following: (a) Adaptation to chromatic light occurs on at least two levels and is a result of both monocular and binocular processes; (b) contrast adaptation can be caused by binocular contrast and builds up; and (c) the monocular and binocular processes for adaptation to chromatic light exhibit different temporal characteristics. The neural visual system adapts to coloured light at multiple levels. These include (a) the transient level of the photochemical receptors that yield lightness and chromatic adaptation, which tunes the centroid of the stimulus variance; (b) the molecular post-receptor level at which spatial contrast from the inputs of each eye is calculated; and (c) a sustainable binocular level that compares binocular inputs and calculates binocular contrast. The after-effects of adaptation to chromatic light are complex and may be affected in different ways by multiple chromatic systems.

In the present study, we aimed to determine whether adaptation to coloured light is achieved not only via photoreceptors in the retina and monocular contrast adaptation, but also by a binocular process that may occur at the level of the cerebral cortex. Our results demonstrated that total retinal exposure was identical for both adaptation conditions, indicating that the duration of photoreceptor adaptation may have been equivalent for both adaptation conditions. Therefore, the difference between these two adapting conditions must be due to differences in the duration of the remaining stage of colour information processing. Because it is known that photoreceptor adaptation does not exhibit interocular transfer, our data suggest that these after-effects were caused by contrast adaptation, which has been reported to exhibit interocular transfer (Blake et al., 1981; Clifford & Weston, 2005; Webster & Mollon, 1994).

The stimulus used to investigate contrast adaptation usually involves a spatial arrangement of lightness or chromatic contrast, such as a target stimulus on a pedestal, Gabor patches, or sinusoidal gratings. The adapting stimulus in this study was a uniform field of chromatic light, and the test stimulus was constant for both adaptation conditions. The only possible cause of contrast in this case was binocular contrast, which has been reported to yield contrast adaptation in colour perception in very few studies. In the anti-phase adaptation condition, the observer was continuously exposed to adapting light through one eye, with the other eye unexposed to any stimulus. However, in the in-phase condition, the observer was constantly exposed to the same stimuli through both eyes (i.e., binocular contrast may not have been present). Therefore, it is reasonable to propose the existence of a binocular neural mechanism that compares and calculates contrast based on information obtained through both eyes, and that this mechanism would affect the after-effects of chromatic contrast adaptation measured through one eye.

The after-effects of photoreceptor adaptation are known to be very ephemeral, typically lasting for only a few seconds (Rinner & Gegenfurtner, 2000), making it difficult to measure a selective decrease in the sensitivity of the three types of retinal photoreceptors. Although this suggests that the after-effects of photoreceptor adaptation would expire within 15 s, the after-effects observed in our experiment were very persistent, indicating that they were caused by contrast adaptation rather than photoreceptor adaptation. A similar adaptation effect, known as the orientation-contingent colour after-effect (i.e., the McCollough effect), can last for more than 24 h (Sheth & Shimojo, 2008; Skowbo, Gentry, Timney, & Morant, 1974). Although the long duration and opposing chromatic after-effect of the McCollough effect suggest that it is related to the chromatic contrast effect, research has indicated that the McCollough effect does not exhibit interocular transfer (Allan & Siegel, 1991).

We believe that participants exposed to the anti-phase condition underwent long-term adaptation, such that the adaptation effects that occurred in each eye were temporally summed together, and that continuous adaptation occurred via a binocular process. In agreement with this hypothesis, previous studies have reported that adaptation involving higher cortical mechanisms is cumulative (Belmore & Shevell, 2011; Dong et al., 2014).

Our results indicated that retinal receptors are relevant to chromatic adaptation; more specifically, that chromatic adaptation involves processes in addition to binocular cortical mechanisms. Measurement of the V1 response on functional magnetic resonance images during adaptation to chromatic light confirms that chromatic adaptation occurs at the cone photoreceptor level (Wade & Wandell, 2002). However, involvement of a higher cortical mechanism involving binocular neurons during adaptation to chromatic light plays a key role in determining the intensity of the after-effect in long-term contrast adaptation. The results of our study indicate that the human visual system likely exhibits a mechanism that continuously adapts in response to the stimuli received, independent of the eye that is adapted, and that the effects of adaptation are cumulative.

The main limitation of the present study is that our methodology was unable to identify the precise loci of the chromatic adaptation mechanism following binocular adaptation. However, we aim to identify these loci in future studies using cortical imaging techniques.

## 5. Conclusions

In the present study, we aimed to confirm the role of central mechanisms in processing input from both eyes during chromatic adaptation.

We compared two adaptation conditions; one anti-phase, in which eyes on either side were exposed to chromatic light alternately, and the other in-phase, in which eyes were exposed simultaneously. Because the after-effect in the in-phase condition was greater than that in the anti-phase condition, with exposure durations of each eye identical, we infer the involvement of post-retinal binocular processes in chromatic adaptation.

Although we were unable to fully explain the instability of the direction of hue (i.e., positive and negative after-effects) in the present study, our results suggest that chromatic light adaptation can be explained using a multi-stage model in which chromatic adaptation processes occur at both photoreceptor and cortical levels.

## 6. Declarations of interest

None.

## Acknowledgements

The authors wish to acknowledge Dr. John Mollon, Professor of Visual Neuroscience, Cambridge University, for his gentle and helpful suggestions in interpreting the significance of the results of this study. Further, we would like to thank the editor, Dr. Martin, and two anonymous reviewers for detailed and helpful suggestions regarding an earlier version of the manuscript.

## Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

## References

Allan, L. G., & Siegel, S. (1991). Characteristics of the indirect McCollough effect. *Perception & Psychophysics, 50*, 249–257. https://doi.org/10.3758/BF03206748.

Barrionuevo, P. A., Matesanz, B. M., Gloriani, A. H., Arranz, I., Issolio, L., Mar, S., & Aparicio, J. A. (2018). Effect of eccentricity and light level on the timing of light adaptation mechanisms. *Journal of the Optical Society of America A, Optics, Image Science, and Vision, 35*, B144–B151. https://doi.org/10.1364/JOSAA.35.00B144.

Belmore, S. C., & Shevell, S. K. (2011). Very-long-term and short-term chromatic adaptation: Are their influences cumulative? *Vision Research, 51*, 362–366. https://doi.org/10.1016/j.visres.2010.11.011.

Blake, R., & Overton, R. (1979). The site of binocular rivalry suppression. *Perception, 8*, 143–152. https://doi.org/10.1068/p080143.

Blake, R., Overton, R., & Lema, S. S. (1981). Interocular transfer of visual aftereffects. *Journal of Experimental Psychology: Human Perception and Performance, 7*, 367–381. https://doi.org/10.1037/0096-1523.7.2.367.

Clifford, C. W. G., & Weston, E. (2005). Aftereffect of adaptation to Glass patterns. *Vision Research, 45*, 1355–1363. https://doi.org/10.1016/j.visres.2004.12.016.

Cooke, J. E., King, A. J., Willmore, B. D. B., & Schnupp, J. W. H. (2018). Contrast gain control in mouse auditory cortex. *Journal of Neurophysiology, 120*, 1872–1884. https://doi.org/10.1152/jn.00847.2017.

Dong, X., Engel, S. A., & Bao, M. (2014). The time course of contrast adaptation measured with a new method: Detection of ramped contrast. *Perception, 43*, 427–437. https://doi.org/10.1068/p7691.

Eisner, A., & Enoch, J. M. (1982). Some effects of 1 week's monocular process exposure to long-wavelength stimuli. *Perception & Psychophysics, 31*, 169–174. https://doi.org/10.3758/BF03206217.

Fairchild, M. D., & Reniff, L. (1995). Time course of chromatic adaptation for color-appearance judgments. *Journal of Optical Society of America A, 12*, 824–833. https://doi.org/10.1364/JOSAA.12.000824.

Hecht, S. (1928). On the binocular fusion of colors and its relation to theories of color vision. *PNAS, 14*, 237–241. https://doi.org/10.1073/pnas.14.3.237.

Hovis, J. K. (1989). Review of dichoptic color mixing. *Optometry and Vision Science, 66*, 181–190.

Howlett, M. H. C., Smith, R. G., & Kamermans, M. (2017). A novel mechanism of cone photoreceptor adaptation. *PLoS Biology, 15*, e2001210. https://doi.org/10.1371/journal.pbio.2001210.

Huchzermeyer, C., Martins, C. M. G., Nagy, B., Barboni, M. T. S., Ventura, D. F., Costa, M. F., & Kremers, J. (2018). Photoreceptor-specific light adaptation of critical flicker frequency in trichromat and dichromat observers. *Journal of the Optical Society of America A, Optics, Image Science, and Vision, 35*, B106–B113. https://doi.org/10.1364/JOSAA.35.00B106.

Hunt, R. W. G. (1950). The effects of daylight and tungsten light –adaptation on color perception. *Journal of The Optical Society of America, 40*, 362–370. https://doi.org/10.1364/JOSA.40.000362.

Keller, A. J., Houlton, R., Kampa, B. M., Lesica, N. A., Mrsic-Flogel, T. D., Keller, G. B., & Helmchen, F. (2017). Stimulus relevance modulates contrast adaptation in visual cortex. *eLife, 6*. https://doi.org/10.7554/eLife.21589.

King, J. L., Lowe, M. P., & Crowder, N. A. (2015). Contrast adaptation is spatial frequency specific in mouse primary visual cortex. *Neuroscience, 310*, 198–205. https://doi.org/10.1016/j.neuroscience.2015.09.037.

Liu, J. K., & Gollisch, T. (2015). Spike-triggered covariance analysis reveals phenomenological diversity of contrast adaptation in the retina. *PLoS Computational Biology, 11*, e1004425. https://doi.org/10.1371/journal.pcbi.1004425.

MacLeod, D. I. A., & Boynton, R. M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America, 69*, 1183–1186. https://doi.org/10.1364/JOSA.69.001183.

McDermott, K. C., Malkoc, G., Mulligan, J. B., & Webster, M. A. (2010). Adaptation and visual salience. *Journal of Vision, 10*, 17. https://doi.org/10.1167/10.13.17.

Nayatani, Y., Hashimoto, K., Takahama, K., & Sobagaki, H. (1987). A nonlinear color-appearance model using estévez-hunt-pointer primaries. *Color Research & Application, 12*, 231–242. https://doi.org/10.1002/col.5080120504.

Neitz, J., Carroll, J., Yamauchi, Y., Neitz, M., & Williams, D. R. (2002). Color perception is mediated by a plastic neural mechanism that is adjustable in adults. *Neuron, 35*, 783–792. https://doi.org/10.1016/S0896-6273(02)00818-8.

O'Shea, R. P., & Crassini, B. (1981). Interocular transfer of the motion after-effect is not reduced by binocular process rivalry. *Vision Research, 21*, 801–804. https://doi.org/10.1016/0042-6989(81)90177-2.

Rinner, O., & Gegenfurtner, K. R. (2000). Time course of chromatic adaptation for color appearance and discrimination. *Vision Research, 40*, 1813–1826. https://doi.org/10.1016/S0042-6989(00)00050-X.

Sheth, B. R., & Shimojo, S. (2008). Adapting to an aftereffect. *Journal of Vision, 8*(29), 1–10. https://doi.org/10.1167/8.3.29.

Skowbo, D., Gentry, T., Timney, B., & Morant, R. B. (1974). The McCollough effect: Influence of several kinds of visual stimulation on decay rate. *Perception & Psychophysics, 16*, 47–49. https://doi.org/10.3758/BF03203248.

Stockman, A., & Sharpe, L. T. (2000). The spectral sensitivities of the middle- and long-wavelength sensitive cones derived from measurements in observers of known genotype. *Vision Research, 40*, 1711–1737. https://doi.org/10.1016/S0042-6989(00)00021-3.

Vergeer, M., Mesik, J., Baek, Y., Wilmerding, K., & Engel, S. A. (2018). Orientation-selective contrast adaptation measured with SSVEP. *Journal of Vision, 18*, 2. https://doi.org/10.1167/18.5.2.

Wade, N. J. (2018). The disparate histories of binocular vision and binaural hearing. *Journal of the History of the Neurosciences, 27*, 10–35. https://doi.org/10.1080/0964704X.2017.1347389.

Wade, A. R., & Wandell, B. A. (2002). Chromatic light adaptation measured using functional magnetic resonance imaging. *The Journal of Neuroscience, 22*, 8148–8157. https://doi.org/10.1523/JNEUROSCI.22-18-08148.2002.

Webster, M. A. (1996). Human colour perception and its adaptation. *Network, 7*, 587–634. https://doi.org/10.1088/0954-898X_7_4_002.

Webster, M. A., & Mollon, J. D. (1994). The influence of contrast adaptation on color appearance. *Vision Research, 34*, 1993–2020. https://doi.org/10.1016/0042-6989(94)90028-0.

Webster, M. A., & Wilson, J. A. (2000). Interactions between chromatic adaptation and contrast adaptation in color appearance. *Vision Research, 40*, 3801–3816. https://doi.org/10.1016/S0042-6989(00)00238-8.

Werner, A., Bayer, A., Schwarz, G., Zrenner, E., & Paulus, W. (2010). Effects of ageing on postreceptoral short-wavelength gain control: Transient tritanopia increases with age. *Vision Research, 50*, 1641–1648. https://doi.org/10.1016/j.visres.2010.05.004.

Zhuang, X., & Shevell, S. K. (2015). Monocular and binocular mechanisms mediating flicker adaptation. *Vision Research, 117*, 41–48. https://doi.org/10.1016/j.visres.2015.08.020.