

What determines unique yellow, L/M cone ratio or visual experience?

Yasuki Yamauchi^{*a}, David R. Williams^a, David H. Brainard^b, Austin Roorda^c, Joseph Carroll^d,
Maureen Neitz^d, Jay Neitz^d, Jack B. Calderone^b, and Gerald H. Jacobs^b

^aUniversity of Rochester, ^bUniversity of California Santa Barbara,

^cUniversity of Houston, ^dMedical College of Wisconsin

ABSTRACT

Unique yellow is considered to represent the equilibrium point of the red-green opponent chromatic mechanism. There are several hypotheses that attempt to explain how this equilibrium point is established. The determinant for unique yellow, however, has not yet been clarified. Here we explored whether the L/M cone ratio or visual information determines unique yellow. If the former is the case, we expect that subjects with large differences in their L/M cone ratio would set different spectral lights to appear as unique yellow. The results of such an experiment, however, did not show a substantial difference in the value of unique yellow for two subjects with very different cone ratios. On the other hand, if the latter is the case, unique yellow should change when altering the chromaticity of the surrounding visual environment. To test this hypothesis, we conducted long-term adaptation experiments, in which subjects spent 8 to 12 hours in a chromatically altered environment. A significant shift of unique yellow was observed after spending time in such an environment for several days. These results indicate that the red-green opponent channel includes a plastic normalization mechanism that adjusts its balance point based on visual experience.

Keywords: color vision, unique yellow, long-term adaptation, chromatic, aftereffect, cone ratio, plasticity, normalization process

1. INTRODUCTION

What determines the perception of color?

The normal human eye has three classes of cones which differ in spectral sensitivity: long- (L-), middle- (M-), and short- (S-) wavelength sensitive cones. The perception of color is determined primarily by the relative magnitude of the signals from these cones. It has been recently reported that the relative number of the three cone classes in the retina varies from person to person.¹ This variability in cone ratio may affect the perception of color, but this remains controversial.^{2,3}

If some mechanism in the visual system could compensate for these differences to stabilize color perception, it could account for the results reported by several studies which indicate that people have similar color perception. Such a mechanism could be either a plastic mechanism controlled by visual experience, or a hard-wired mechanism that acted during development.

To clarify what controls color perception, two experiments were conducted. We measured unique yellow as a method for assessing color perception. Unique yellow is the wavelength of light that appears neither reddish nor greenish. It is considered to express the equilibrium point of the red-green opponent color channel. In Experiment 1, spectral unique yellow was measured on subjects whose cone mosaics were characterized with an adaptive optics system. In Experiment 2, the effects of long-term chromatic adaptation were measured on unique yellow. Experiment 1 is reported in more detail elsewhere.⁴

2. EXPERIMENT 1: UNIQUE YELLOW OF SUBJECTS WITH KNOWN L/M RATIOS

2.1 Methods

Two male observers were used in this experiment. These observers were chosen because the relative numbers of L and M cones in their retinas had previously been established. The imaging procedure used to identify individual L, M, and S cones in the retinal mosaic combines high-resolution imaging and retinal densitometry. For each observer, the eye's wave aberration was measured with a Hartmann-Shack wavefront sensor and subsequently compensated for with a deformable mirror. This corrective procedure makes it possible to resolve the mosaic of cone photoreceptors. Identification of the type of each cone was done by comparison of the images acquired before and after selective bleaching of cone photopigment with 650- and 470-nm light. The two observers had a large difference in L/M cone ratio. AN had a L/M cone ratio of 1.15, while that of subject JW was 3.79.

The wavelength perceived as uniquely yellow was measured in a Maxwellian-view apparatus. Observers viewed a 0.52-deg circular spot with their right eye. The stimulus spot was located at 1 deg in the nasal retina, corresponding to the location where the L/M cone ratio had been established for both observers. The retinal illuminance was approximately 50 td. A small, dim spot served as a fixation point. The stimulus was viewed in an otherwise dark surround. The test stimulus was presented repeatedly for 0.5 sec with an interstimulus interval of 3.5 sec. Before starting a session the observer dark adapted for 1 min. During a session, 20 trials of each of five wavelengths were presented in a random order, for a total of 100 trials. On each trial, the observer made a forced-choice judgment as to whether the test flash appeared reddish or greenish. The five wavelengths used in the forced choice experiment with an interval of 1 nm were determined based on the preliminary measurement conducted using the method of adjustment, in which the observer set the wavelength of the test flash so it appeared to be neither reddish nor greenish.

For each session, the wavelength of unique yellow was determined as the 50% point of a psychometric function fit to the forced-choice data. This value was averaged over four sessions for observer AN and two sessions for observer JW to determine a mean value for each observer.

2.2 Results and discussion

The wavelength of unique yellow was 576.8 nm for AN (standard error, 0.6 nm) and 574.7 nm for JW (standard error: 0.7nm). Ciccone presented a simple additive model of how the wavelength of unique yellow could be expected to vary with the relative numbers of L and M cones². This model is based on the ideas that (a) a stimulus appear as neither red nor green when the output of a linear red-green mechanism is zero and that (b) the contribution of L and M cones to the red-green mechanism varies in proportion to their relative numbers. This model may be expressed as

$$(N_L / N_M)L(\lambda_y) - k M(\lambda_y) = 0,$$

where λ_y is the wavelength of unique yellow, N_L / N_M is the L/M cone ratio, k is a constant that describes any neural factors that govern the relative contribution of L and M cones to the red-green mechanism, and the functions $L(\lambda)$ and $M(\lambda)$ represent the L and M cone spectral sensitivities. We set k here so that unique yellow for an observer having a relative cone ratio of two would be 580 nm.

Figure 1 shows both the experimental results (solid circles) and the theoretical prediction by the additive model described above (gray solid line). If unique yellow were solely determined by the relative cone ratio, the unique yellow of AN should be 602 nm, while that of JW should be 518 nm. Although the difference in unique yellow between two subjects is 2.1 nm and is in the right direction, it is smaller by a factor of 40 than the predicted difference. Shown also are unique yellow settings and ERG-derived L/M cone ratio estimates from 15 color normal males (open triangles).⁵ There is no correlation between cone ratio and unique yellow settings. These results support the idea that the relative cone ratios are not primary determinant of the balance point of the red-green opponent channel.

3. EXPERIMENT 2: LONG-TERM CHROMATIC ADAPTATION

The first experiment showed that the balance point of the red-green opponent channel is not strongly influenced by the L and M cone ratio. This result suggests that color vision is either a hard-wired post-receptoral mechanism or an experience-based plastic mechanism that stabilizes unique yellow against changes in cone ratio. In both cases, individual differences in cone ratio would not be expected to influence color perception. However, to determine what the stabilizing mechanism is, we can simply alter the chromatic properties of a subject's visual environment. If the chromatic mechanism is plastic and driven by visual information, then unique yellow should show a shift after the eye has been exposed to such an altered environment. On the other hand, if a hard-wired mechanism is responsible for setting color perception, then altering the incoming visual information should not be expected to induce any long-term changes in color perception. We conducted a long-term chromatic adaptation experiment to determine which of these outcomes occurred.

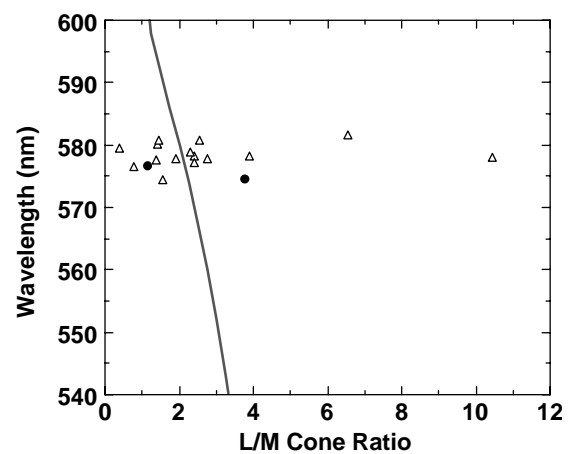


Fig. 1 Experimental data and predicted unique yellow by an additive model

3.1 Methods

In this experiment, the adult subjects spent a part of the day in an altered chromatic environment. Two male subjects and one naive female subject, all having normal color vision, were used in this experiment. We used tinted contact lenses to provide a chromatically altered environment. Contact lenses were tinted with a commercially available dye kit. Lenses were designed with similar transmission curves as Kodak Wratten filters 29 and 58 (red and green).

Before starting the experiment, the subject's unique yellow was collected for several days and served as a baseline. Once the adaptation started, the procedures were conducted on a daily schedule, as shown in Figure 2. Unique yellow was measured at the beginning of each day prior to being exposed to an altered chromatic environment. The subject then spent 8 or 12 hours in that condition. After adaptation, the subject spent the rest of the day in a normal environment. The activity of the subjects was not restricted at all during and after the adaptation. The interval between the termination of daily adaptation and the measurement of unique yellow the next day was about 12 to 16 hours. Since it is well known that the effects of short-term chromatic adaptation decay in minutes, 12 to 16 hours should be more than long enough for these short-lived aftereffects to fade away.

The same apparatus used in experiment 1 was employed to measure unique yellow. The method of adjustment was adopted in this experiment. The stimulus was presented to the fovea. Five trials were conducted in each session, after 5 minutes of dark adaptation. Each trial started with a monochromatic light that was clearly reddish or clearly greenish, and the subject adjusted the wavelength of this light until it appeared neither reddish nor greenish.

3.2 Results and discussion

Figure 3 shows the results obtained from two subjects, YY and EM. Subject YY adapted for 8 hours each day for more than 3 weeks, while subject EM adapted for 12 hours a day over a 10-day period. Open symbols correspond to data collected when the subjects were not exposed to an altered environment. Solid circles and squares represent data collected during the adaptation to the red and green environments, respectively.

When the subjects started the adaptation, unique yellow began to shift towards longer wavelengths even though the measurement of unique yellow was conducted 12 to 18 hours after the adaptation period. Unique yellow shifted so much that wavelengths previously called red now appeared green and vice versa. For approximately the first 30 minutes after immediately completing a daily adaptation of 8 or 12 hours, both subjects reported that the natural scene looked greenish or reddish, depending on which color adaptation was conducted. The shift of unique yellow, however, did not proceed in proportion to the period of adaptation. For YY, unique yellow did not show a further shift after a period of two weeks. EM's unique yellow also appeared to come to an asymptote after a week of adaptation. However, it is not clear if EM's unique yellow might have continued to shift if she had a longer adaptation period. After

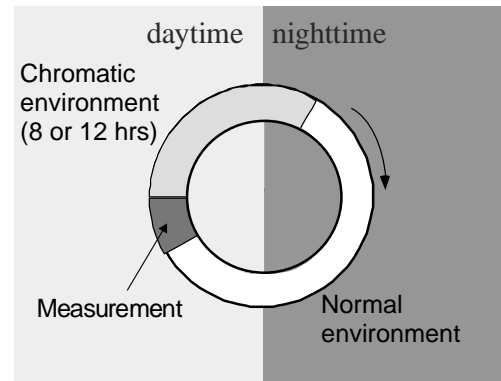


Fig. 2 Schematic representation of the daily schedule for the long-term adaptation experiment.

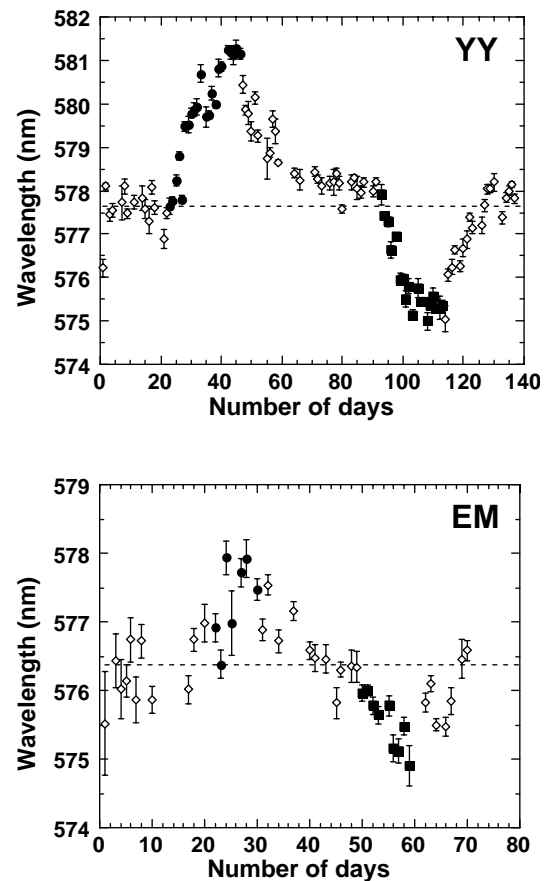


Fig. 3 The results obtained in the long-term adaptation experiment.

termination of the adaptation, unique yellow showed a steady recovery towards the baseline value and it took more than 2 weeks to come to an asymptote. For YY, a residual shift of unique yellow existed even a month after the adaptation. The third subject, whose results are not presented, showed the same trends when he conducted the red adaptation condition. Similar trends could also be observed in the green environment. For YY, unique yellow kept shifting for the first two weeks of adaptation and leveled off for the remainder of the test period, it then took almost two weeks to recover back to baseline. These results show that chromatic adaptation can cause a long-lasting effect on the perception of unique yellow, which differs in time course from the well-known, short-lived aftereffects of chromatic adaptation.^{6,7}

4. DISCUSSION

In agreement with previous data on carriers of color vision defects^{8,9}, our results show that, in color normals, variation in unique yellow is not explained solely by the variation in L/M cone ratio. The lack of large variation of unique yellow can be accounted for if the opponent color channel adjusts its balance point based on visual experience. Our empirical results obtained in the long-term adaptation experiment support this hypothesis. Chromatic adaptation was shown to cause a long-lasting but reversible effect in the perception of unique yellow. The long-lasting effects suggest that color vision is mediated by a plastic normalization process, perhaps like that proposed by Pokorny and his colleagues, in which the mean chromaticity of the environment plays an important role in determining the equilibrium point of the red-green opponent mechanism.¹⁰ This normalization mechanism may operate throughout the entire lifespan, as such plasticity could account for why there is little difference in perceived color appearance for observers of different ages, even though the optical quality of lens changes over time.¹¹ Our results indicate that it can take a long time to induce changes in color perception and that these changes can persist for weeks, even after returning to a natural, non-chromatically altered environment.

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