Illumination-evoked plasticity

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Abstract

The hallmark of any dynamic system lies in its ability to rapidly modify its most basic architecture in response to external demands. Under certain conditions, the trichromatic system, vision which is based on a functioning long-wave (L), middle-wave (M) and short-wave (S) spectral types of cone photoreceptors, encounters a visual scene in which the illumination is ill-defined. As a consequence of this ambiguity, the chromaticity of the objects within the visual scene appears ambiguous. To resolve this ambiguity, one of two illumination priors – $Prior_S$ or $Prior_{L+M}$ – is recruited by the trichromatic system to infer which incident illuminant to discount. However, it is poorly understood whether the trichromatic system is able to switch between illumination priors across different object conditions. Here, human trichromats were presented with two classes of objects – either a circular patch or natural fruit objects – tinted with a shade of color in order to mimic the effects of a poorly illuminated visual scene, and asked to adjust the chromaticity of each object until it appeared devoid of any hue in the DKL color space which spans two chromatic opponent axes – the S–(L+M) and L–M axis – and a luminance axis – the L+M axis. The following observations were made: (i) across objects, adjustments were dispersed along the S–(L+M) axis, which daylight illumination is known to vary along [1]; (ii) across subjects, where an illumination prior was recruited for one class of objects, the opponent prior was recruited for the other class of objects; (iii) this remarkable ability to switch between priors across different conditions – while present amongst all trichromats – was weaker among trichromats of older age [2]. These results suggest that internal illumination priors are neither sex nor chronotype specific and that the ability to switch between illumination priors is age-dependent.

Keywords: color vision, illumination prior, perceptual constancy, plasticity, aging

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Introduction

An array of distal properties contributes to the proximal retinal image – illumination source, the transmittance priorities, the reflectance properties of the object, the organism's relative viewing orientation and the optics of its eye, along with other factors which actively modulate the incoming retinal signal. This signal, however, is insufficient with respect to the inverse problem of perception, that is inferring the properties of the retinal image from these distal properties [3]. To this end, perception relies on an array of inferences and assumptions derived from the organism's prior experiences, which are overtime integrated into the organism's most basic architecture [4-9]. Of particular interest is whether these inferences (or internal priors) the mammalian visual system has derived during its development, are presently being recruited by the human visual system [10-13].

Consider Figure 1A. The visual scene is homogeneously illuminated under a neutral illumination. Because of this, the proximal retinal image embedded within this visual scene will appear to the normal human trichromat as having a brownish and bluish appearance. However, in Figure 1B, within the same exact scene, now illuminated under a warmer illumination, the image will have a white and yellowish appearance. Under an opposing illumination, as depicted in Figure 1C, the appearance of these objects is once again displaced, in this case, towards the opponent hue of yellow and white, that it is, blue and black. Figures 1A-1C depict cases where the illumination illuminating the visual scene is well-defined. However, in Figure 1D, the illumination source is ill-defined, that is, both warm and cool. Naturally, the chromaticity of the retinal image within this scene will appear ambiguous, specifically, in one of three sets of color: blue and brown, blue and black and yellow and white.

Figure 1. Visual scenes illuminated under different illumination sources: (A) neutral illumination, (B) bluish illuminant, (C) yellowish illuminant, (D) bluish and yellowish illuminant.

To provide a relatively stable representation of object's color caused by the ambiguously illuminated visual scene in cases like Figure 1D, the trichromatic system must rapidly infer from a set of internal priors it possesses the incident illuminant to discount [14-15]. The residual illuminant is eventually recruited as the primary illuminant defining the chromaticity of the object within that very scene. The residual illuminant assigned as the primary illuminant differs across subjects, specifically in the case of Figure 1D which, by virtue of the possible illuminants one is able to discount, will give rise to a certain degree of variability in perception, as it has been observed with the dress phenomenon [16-21].

It is poorly understood how the trichromatic system selects which illumination to discount under these conditions. However, more recent studies have put forth an incredibly novel and compelling hypothesis [22,23,18]. Considering that the mammalian visual system, specifically the molecular machinery within the retina (i.e. rhodopsin molecules) which enables the detection of photons of light [24], as well as the thalamic and cortical circuits which subserve visual perception (e.g. lateral geniculate nuclei and striate cortex) developed under daylight illumination which routinely fluctuates from shorter wavelength of light frequencies (cooler illumination) in the morning towards longer wavelength of light during the course of the day (warmer illuminant), the human visual system possesses one of two illumination priors - $Prior_S$ (blue) or $Prior_{L+M}$ (yellow) which project along the S–(L+M) (blue-yellow) axis, which daylight illumination is known to vary along [1, 25]. These internal priors, presumably derived during the development of the visual system, are used to decide which illuminant should be discounted. This means that, in cases like Figure 1D, the visual system which is excessively exposed and thus preferentially tuned to short-wave illumination ($Prior_S$), swiftly discounts the cool illuminant, resulting in a whitish and yellowish percept, that is, a projection towards the L+M pole (yellow) of the S–(L+M) axis. Inversely, when a subject possesses a $Prior_{L+M}$, the warmer illuminant is discounted, resulting in a blackish and bluish percept, that is, a projection towards the S pole (blue) of the S–(L+M) axis. Finally, in the most extreme case, the visual system tuned to both illuminant types discounts both the warm and cool illuminant, resulting in a brownish and bluish percept.

While this hypothesis seems plausible, the jury is still out as to whether these internal illumination priors are in fact represented within the visual system's most basic compartments. Specifically, it is not known whether the human visual system is only capable of possessing one of the two internal priors or both. One way to empirically address this question is to measure the chromatic perception for two distinct classes of objects – with the illumination under which they are presented being equally ill-defined – so as to examine whether different types of priors are recruited for different classes of objects. If subjects can only recruit a single prior and never both across different object conditions, then chromatic perception for both classes of objects should be projected towards a single direction along the S–(L+M) (blue-yellow) opponent axis. Inversely, if the visual system of a given subject is plastic to some degree, that is, able to

recruit both types of priors at will, then chromatic perception should be projected to both directions along this axis.

To foreshadow, in the experiment, chromatic perception for both classes of objects, i.e. circular patch in part 1 and natural fruit objects in part 2, were almost always projected along the S−(L+M) opponent axis. Specifically, in part 1, two types of subjects emerged – those who systematically perceived the circular patch having a blueish appearance and those who perceived the circular patch as having a yellowish appearance. In part 2, the opposite effect was observed, with subjects who perceived the circular patch as has having a blueish appearance, reporting the natural fruit object as having a yellowish appearance, and vice versa. This suggest that a given subject is able to possess two internal illumination priors and it is able to recruit different priors for different classes of objects for which the illumination is equally ill-defined, providing separate and stable chromatic percept of a given object.

Methods

Subjects

Twenty-five naive subjects concurred to participate in part 1 and part 2 of the experiment. There was a total of fifteen women and ten men with a mean age of 23.11 and an SD of 3.98. Each subject was tested for normal to corrected-to-normal visual acuity and normal color vision using the Ishihara color plates. The protocol for this study was approved by the Johns Hopkins University Homewood IRB.

Apparatus

Stimuli were presented on a Dell D1526HT cathode ray tube (CRT). Gamma correction and color space calibration (computed using spectral distribution of the CRT's phosphor channel and the Smith & Pokorny 2-deg cone fundamentals [26]) were accomplished using standard procedures [27,28] and utilizing a UDT Instruments model 370 optometer with a model 265 photometric filter (mounted atop a Dolica 68" Lightweight Tripod) and a Lighting Passport Pro spectroradiometer. The CRT was firmly positioned 30cm behind a neutral wall which subtended 81 × 42°, allowing the concealment of the light source. CRT was driven by a NVIDIA Quadro FX 580 graphics card with a color resolution of 8 bits per channel. The spatial resolution of the CRT during the duration of the experiment was 1280 × 1024 pixels with a refresh rate of 85 Hz (11.76 ms per frame). The Judd correction CIE xyY values for the red, green and blue primary were (x=0.631 y=0.337 Y=20.451) (x=0.295 y=0.600 Y=52.743) (x=0.148 y=0.065 Y=6.457) respectively. Directly at the center of the wall was an opening which subtended 10.6 × 9° [29]. The interior region of the viewing tunnel was homogenously painted using a Clarke and Kensington deep matte black acrylic paint, thereby inhibiting any unsolicited shadows or light reflectance. This was later connected to the posterior region of the neutral wall directly to the center of the CRT's phosphorescent surface. At the anterior base of the wall extended 17cm horizontally a trapezoid-shaped hand chamber with the exterior and interior painted deep matte black to prevent any reflectance of keypress or any glossy or self-illuminating objects worn by subjects. Inside the hand chamber was fixedly placed a black

Dell L100 keypress. Attached to the base of the hand chamber was a black adjustable head and chin rest. The chin rest not only allowed for a standardized viewing distance for all subjects at 52 cm, but also a natural demarcation between the left and right-hand. Figure 2A-B presents a photograph of the experimental setup.

Figure 2A-G. Photograph of the apparatus and stimuli (resized for viewing purposes) used in the present study. (A) subject's view during the experiment; (B) the dorsal view of the viewing tunnel which was firmly placed on the front of the CRT; (C) homogenously colored circular patch; (D) banana; (E) pear; (F) foliage; (G) grapes. Each natural fruit object was captured under standard daylight illuminant with the white balance set to 6,500 Kelvin. This prevented any undesired color casting on the photographs.

Stimuli & Procedure

In each trial of part 1 of the experiment, each subject observed a homogenously colored circular patch (3×3°) (see Fig 1B). This object was carefully selected as it is an object which approximates real-world objects to a lesser degree. The luminance of the patch was set to 30 cd/m^2 while the background was set to 28.632 cd/m^2 in order to avoid any color blending strategies [28]. The patch appeared with a tinted shade of color chosen randomly from within the DKL color space. The shade was carefully placed on the surface of the patch in order to create a shadow-like casting on the surface of the object, that is, make it ambiguous, such that at the onset of each trial the subject became less certain about the illuminant source and consequently the chromaticity of the object [30, 31]. Note that this color space used to define the stimuli used in the experiment reported here is modeled after the second stage of color perception, thereby reflecting the preferences of neurons in the Lateral Geniculate Nuclei (LGN) in macaques [32,33]. Furthermore, the subjects' task was to adjust the hue of the patch until it appeared void of any hue. Adjustments were made by the keypress, along the isoluminant L–M (red-green) color opponent axis, using the left arrow and right arrow, or along the isoluminant S–(L+M) (blue-yellow) axis, using the up and down arrows. Subjects were also able to modify the pace by which they preferred to move along each axis, toggling between finer and coarser changes by pressing the 'v' and the 't' keys respectively. If a given participant got lost within the color space, he or she could press the 'q' key, resetting the object to the initial color it was presented in. Finally, upon the completion of an adjustment (pressing the 'a' key), the chromaticity of each individual pixel was scaled to the stimulus' new chromatic position [28]. There were no time constraints on the adjustments.

Trials in part 2 of the experiment were identical to trials in part 1, with two critical exceptions. Firstly, each trial included one of four digitalized photographs of real-world objects (either a banana, pear, autumn leaf or grapes) instead of a circular patch. The banana subtended 6.20° × 4.07°, the grapes, and autumn leaf subtended 4.66° × 4.57° and the pear subtended 4.41° × 5.56°. These objects were set to have the same mean luminance values across their surfaces as the background (28.632 cd/m^2). This class of real-world objects – known and remembered to appear in a canonical color – were selected in order to optimally engage the visual system. Secondly, upon the first appearance in a trial, these objects did not appear in a random hue. Instead, the surface of each object was covertly tinted with a specific hue in different conditions. In the 'canonical' condition, an object appeared with a tint of a canonical hue (e.g. yellowish in the case of a banana). In the 'deuterocanonical' condition, an object appeared in a tint of a hue of a secondary association (e.g. greenish for a banana). In the 'opponent' condition, the item was tinted with a hue situated in the opponent direction from its canonical association (e.g. blueish in the case of a banana). The purpose of placing these tints on the objects' surface was to make the illuminant source ambiguous as well as determine whether subjects would use this tint as an anchor by which they adjusted the chromaticity of the object. Although I call them 'part 1' and 'part 2' their order was counterbalanced in practice across subjects. Each subject completed a total of 8 trials in part 1 and 80 trials in part 2 (equally distributed across objects and conditions).

Figure 3A- B. General procedure for part 1 and part 2: (A) circular patch, (B) natural fruit object

Results

In part 1, chromatic adjustments for the homogenously circular patch were systematically disturbed along the S−(L+M) axis. To confirm this, a line of best-fit was computed, which projected along the S−(L+M) opponent axis, specifically, R^2=0.81, p <0.01 (See Figure 4). Using the horizontal meridian as the chromatic boundary to examine whether two types of cohorts would emerge, one shifted towards the S pole of the S−(L+M) axis and the other shifted towards the (L+M) pole of this axis, each subject's mean chromatic adjustment was computed in part 1 across all trials. The chromatic mean revealed that 14 (⬚=9, ⬚=5) out of the 25 subjects adjusted the patch towards the S pole of this axis to varying degrees. The mean age for this group was 20.28 with an SD of 2.78. The mean chromatic adjustment along the x-axis across all subjects was -0.0999 with SEM of 0.0344, while along the y-axis the mean chromaticity was -0.0785 with a SEM of 0.0257. For the remaining 11 (⬚ =6, ⬚=5) subjects, the mean chromatic adjustments were biased towards the L+M pole of the S−(L+M) axis, while the mean age was 26.27 with SD of 2.24. Here, the mean chromaticity along the x-axis was 0.0062 with SEM of 0.0138, while along the y-axis, the mean chromaticity was 0.0599 with SEM of 0.0135.

Figure 4. Chromatic adjustments across all subjects for part 1.

A best-fit ellipse at a 95% confidence interval was computed in order to assess the directionality of overall mean across each subject within a given cohort [34]. The best-fit ellipse for subjects whose mean chromatic adjustments were below the horizontal meridian was, as expected, orientated towards the S pole with an area of 0.1995 and an eccentricity of 0.8517. For subjects whose mean chromaticity was above the horizontal meridian, the best-fit ellipse was orientated in and around L+M pole with an area of 0.0289 and an eccentricity of 0.8929.

Figure 5. Best-fit ellipse at a 95% confidence interval for part 1 for subjects whose mean chromatic adjustment was below and above the horizontal meridian.

In part 2 chromatic adjustments were also projected along the S−(L+M) opponent axis. Here, $R^2 = 0.68$, p <0.01 (see Figure 6).

Figure 6. Chromatic adjustments across all subjects for part 2.

Similarly to my observation in part 1, the mean chromatic adjustments showed two types of subjects – those whose chromatic adjustments were biased towards the (L+M) pole of the S–(L+M) opponent axis and those whose chromatic adjustments were biased towards the S pole of the S–(L+M) opponent axis. What is of particular interest is that subjects, to varying degrees, systematically adjusted the chromaticity for the class of objects in part 2 towards the opponent direction of their mean chromatic point in part 1. Specifically, for those whose mean chromatic adjustments were biased towards the S pole of the S–(L + M) opponent axis in case of the patch, for natural fruit objects – irrespective of the canonical, deuterocanonical or opponent hue in which they were tinted – average chromatic adjustments were projected towards the L+M pole of the S–(L+M) opponent axis. The best-fit ellipse confirmed this general trend which had an area of 0.027 with an eccentricity of 0.876. The mean chromatic adjustment across all objects along the x-axis was 0.0176 with SEM of 0.0099, while the mean chromatic adjustment along the y-axis was 0.0384 with SEM of 0.0131. For the cohort of subjects whose mean chromatic adjustment was projected towards the L+M pole in part 1, adjustments for natural fruit objects were biased towards the opponent direction, that is, towards the S pole. Here, the best-fit ellipse was projected towards the S pole but not to the same extent as the ellipse projected towards the L+M pole for the previous group of

subjects. The best-fit ellipse demonstrated an area of 0.0162 with an eccentricity of 0.9392. Across all subjects, the mean chromatic adjustment along the x-axis was -0.0044 with SEM of 0.0114, while the mean along the y-axis was 0.0185 with SEM of 0.0111.

Figure 7. Best-fit ellipse at a 95% confidence interval for the cohort who recruited a $Prior_s$ or a $Prior_{L+M}$ in part 1 but the opposing prior in part 2.

The chromatic displacement for each subject with respect to their mean chromatic adjustment in part 1 was computed. It is expected that the vertical and horizontal displacement for the subjects whose mean chromatic adjustments were projected towards the S pole, that is blue, in part 1 would trend towards the positive direction, towards the (L+M), that is yellow, in part 2, and vice versa. For the former cohort results showed that 11 out of the 14 subjects demonstrated a positive displacement along both the horizontal and vertical plane. To confirm the significance of this displacement specifically along the vertical plane, a t-test was conducted. Results showed p-value < 0.05 for 7 out of 14 subjects.

Figure 8. Mean displacement along the vertical and horizontal plane for subjects whose chromatic adjustment was shifted towards blue in part 1.

In turn, for the cohort of subjects with a mean projected towards the L+M pole of the S−(L+M) axis in part 1, 5 out of 11 subjects demonstrated a negative displacement along both the horizontal and vertical plane. For displacement along the vertical plane, results showed p-value <0.05 for 7 out of 11 subjects.

Figure 9. Mean displacement along the vertical and horizontal plane for subjects whose chromatic adjustment was shifted towards yellow in part 1.

General Discussion

Here, I sought to extend the research on how the human visual system stabilizes a visual scene in which the incident illuminant is ill-defined and study its effects on the chromaticity of the objects embedded within that scene. While more recent studies have suggested that the human visual system deals with these cases by recruiting strictly one of two illumination priors — $Prior_s$ or $Prior_{L+M}$ — I investigated whether the human visual system is hard-wired to a single illumination prior or is in fact plastic, that is, able to recruit both types of priors across different conditions. In both part 1 and part 2 of the experiment conducted, subjects systemically adjusted the surface of the circular patch and the natural fruit object along the S−(L+M) axis, which daylight is known to vary along. Most importantly, where subjects exhibited a particular bias for a circular patch towards one direction of this axis, an opposite bias was observed for the natural fruit objects. These results support the general hypothesis that when the human visual system encounters a visual scene in which the illumination is ill-defined, internal illumination priors direct the vision system as to the chromatic property of the illuminant source it is to discount [18].

Secondly, these results are also consistent with previous studies which show that subjects typically fall into two distinct groups – blue and yellow group under certain conditions [16-21]. Here, however, for the first time, I show that subjects are able to recruit both types of prior, as evidenced by the visual system's ability to present a stable but distinct chromatic perception for two different classes of objects.

Furthermore, the results attained suggest that there is no innate group a given subject belongs to; a notion consistent with the general idea that mammalian visual system is able to achieve a remarkable degree of plasticity, especially with experience [35]. To this end, my work does not support the assertion that the type of internal prior one possesses is based on sex [18] or chronotype [36], given that, while they were not asked to report their chronotype, the subjects were able to switch internal prior from part 1 to part 2.

What remains to be addressed, and should be the focus of future studies, is why the displacement for subjects who in part 1 recruited a blue prior, that is, projected towards the L+M pole of the S−(L+M) axis, was of a lesser degree. Here, I hypothesize that this effect is a function of age. Specifically, the aging visual system is less willing to change its most basic architecture, settling upon a single prior to resolve ill-defined conditions. In this case, this reduction in plasticity appears not only efficient but inconsequential, as the older visual system is able to provide a stable representation of the object's color equally to the younger visual system [37-39]. It is also possible that the unwillingness to explore a different prior, namely a yellow prior, is advantageous to the visual system's longevity, considering the known effects of exposure to bluish illumination, namely the promotion of retinal disorders such as Adult Macular Degeneration, which the aging visual system is particularly susceptible to [40]. In all, the achromatic adjustment procedure developed for the study now appears to be a useful tool for further research on illumination priors, and more generally, for investigating possible interactions between priors and its effects on proximal retinal image perception.

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Ethics

This study was approved by the Johns Hopkins University Homewood IRB and conducted in accordance with the principles noted in the Declaration of Helsinki. Informed consent was also obtained for all participants.

Competing interests

I have no competing interests.

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