Spectral memory: Illumination evoked plasticity

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Abstract

Here human trichromats were presented with two classes of objects – a disc and natural fruit objects – tinted with a shade of colour in order to destabilize the perceived illumination, and chromaticity of the retinal image. Each trichromat was instructed to adjust the chromaticity of each object until its surface appeared devoid of any hue in the DKL colour 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, along which daylight is known to vary; (ii) across trichromats, for the disc, adjustments were biased towards the S pole of the S–(L+M) axis for one group, and towards the (L+M) pole for the other group; (iii) for the natural fruit objects, adjustments for both groups systematically converged towards the (L+M) pole. These results suggest that when the core set of priors the visual system relies upon become ill-equipped, illumination priors - PriorS or PriorL+M – for unfamiliar objects, and what I have termed "spectral memory" for familiar objects, are recruited by the visual system, as it attempts to stabilize the chromaticity of the retinal image.

Keyword: Retinal image., Perception, Priors, Daylight illumination, Visual plasticity, Spectral memory

Introduction

An array of distal properties contributes to the proximal retinal image – illumination source, the transmittance properties, 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 components of these distal properties from the retinal image. To this end, perception relies on, not one or two, but a repertoire of implicit assumptions and inferences (or internal priors) many of which have been strongly influenced by the organism's ecological niche during its development, coupled with the organism's daily task, specifically those which heavily rely on a stable chromatic image (e.g. foraging for fruits) [1,2,3].

Consider Figure 1A. Here a simplified snapshot of a poorly illuminated retinal image at an early stage in visual processing is given. If visual processing were to terminate here, the normal trichromatic observer (vision based on L, M, and S cone photoreceptors) will most likely perceive an unstable retinal image, that is, an image which appears to have three sets of colours: yellow and white, blue and brown, and blue and black. This ambiguity however does not make for an efficient visual system, especially in cases when the chromaticity of the retinal image is critical in assessing the state of an external object (e.g. ripe or unripe fruit) or enhances the recognition of an unknown object or visual scene [4]. Aware of this erroneous representation of the retinal image, the visual system must undergo a set of operations in which spectral components included in the illuminant source are discounted, thus stabilizing the retinal image [5]. However, in conditions like Figure 1A, the canonical operations the visual system usually undergoes (e.g. chromatic adaptation), in which the spectral component of the incident illumination discounted is relatively consistent across normal trichromats does not always hold, as it is observed in the dress phenomenon [6,7]. Specifically, when normal human trichromats are instructed to recover the colours perceived in Figure 1A, the retinal image is typically reported as appearing in either yellow and white – 1B, blue and black- 1C, or brown and blue- 1D, which suggest that the spectral component being discounted by the visual system across trichromats is radically inconsistent [8,9].

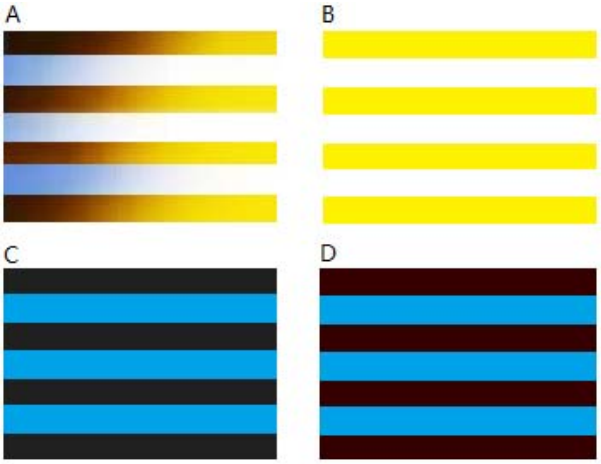

Figure 1. Striking individual differences in perception. A. an uncalibrated retinal image under poorly illuminated conditions, percept the visual system constructed when it elects to discount short-wave illuminant – B, long-wave illuminant – C, or both illuminant – D.

To explain this divergence in perception, recent studies have put forth an incredibly novel and compelling hypothesis [10,11]. 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 , 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 in the morning towards longer wavelength of light during the course of the day, the human visual system may possess one of two illumination priors - *PriorS* (blue) or *PriorL+M* (yellow) which project along the S–(L+M) (blue-yellow) axis, along which daylight illumination is known to vary [12,13]. Consequently, these internal priors under ill-defined conditions are used to stabilize the retinal image. This means that, in cases like Figure 1A, the visual system which is preferentially tuned to short-wave illuminants (e.g. blue skies) expects the spectral composition of the illuminant to be largely composed of the bluish spectrum, which leads it to discount the bluish component of the illuminant, thus constructing a whitish and yellowish percept, that is, a projection towards the L+M pole (yellow) of the S–(L+M) axis. Inversely, for other trichromats preferentially tuned to long-wave illuminants (e.g. incandescent light) the yellowish spectrum of the illuminant is quickly 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 bluish and yellowish spectrum of the 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 on the perceptual domain of the visual system. Specifically, it is not known whether the 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 of familiar real-world objects, many of which populate the trichromat's day to day environment versus objects which do not (e.g. circular

disc), 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. The rationale here is that the visual system which is excessively exposed to long-wave illuminants under real-world conditions will naturally discount the yellowish spectrum of the illuminant, thus shifting perception towards a bluish percept for the real-world objects. Inversely, for the opposing class of objects– the circular disc–, considering that these objects do not approximate familiar objects in the real-world, the illumination prior recruited in stabilizing the colour of these class of objects in the most extreme case may be opposed to the observed primary illumination prior. Alternately, it is also possible that among the trichromats who are tested, specifically those who are excessively exposed to natural illumination (e.g. California and Arizona natives), when presented with real-world objects, these groups of trichromats could demonstrate a yellowish bias; while for the circular disc, opponent biases towards a bluish percept would most likely be observed.

To foreshadow the results in the experiments which are reported here, when normal human trichromats were instructed to adjust the surface of a set of natural fruit objects or a circular disc until it appeared devoid of any hue, chromatic adjustments were almost always projected along the S–(L+M) opponent axis. Specifically, two groups emerged. The first group of trichromats systematically adjusted the surface of the circular disc to the (S) bluish pole of the S–(L+M) opponent axis, while the natural fruit objects were adjusted towards the L+M pole of the S–(L+M) opponent axis – a remarkable demonstration of visual plasticity in the adult visual system. As for the second group, chromatic adjustments for the circular disc were projected towards the (L+M) of S–(L+M) opponent axis. And while the degree of bias towards the S pole was significant for individual trichromats, overall chromatic adjustments across trichromats largely remained in the (L+M) pole for the natural fruit objects. These results suggest that the human visual system possesses only a single internal illumination prior at a time, which it principally recruits under ill-defined conditions as it is reflected in the chromatic adjustments for the unfamiliar objects (circular disc). Results further suggest that under these same illuminant conditions, for the familiar objects (natural fruits), the human visual system is able to undergo a mechanism which has never been observed in humans until now Specifically, it appears that the human visual system actively records the spectral composition of the illuminant source, which real-world objects are typically illuminated under, and under poorly illuminated conditions, recruits this "spectral memory" to help stabilize the chromaticity of the retinal image.

Method

Human trichromats

Twenty-five naive normal human trichromats concurred to participate in part 1 and part 2 of the experiment. There was a total of fifteen females and ten males with a mean age of 23.11 and an SD of 3.98. Each trichromat was tested for normal to corrected-to-normal visual acuity and normal colour vision

using the Ishihara colour 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 colour space calibration (computed using spectral distribution of the CRT's phosphor channel and the Smith & Pokorny 2-deg cone fundamentals) were accomplished using standard procedures [14,15] 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 colour 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° [16]. 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 trichromats. 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 across trichromats at 52 cm, but also allowed for a natural demarcation between the left and right-hand. Figure 2A-B presents a photograph of the experimental setup.

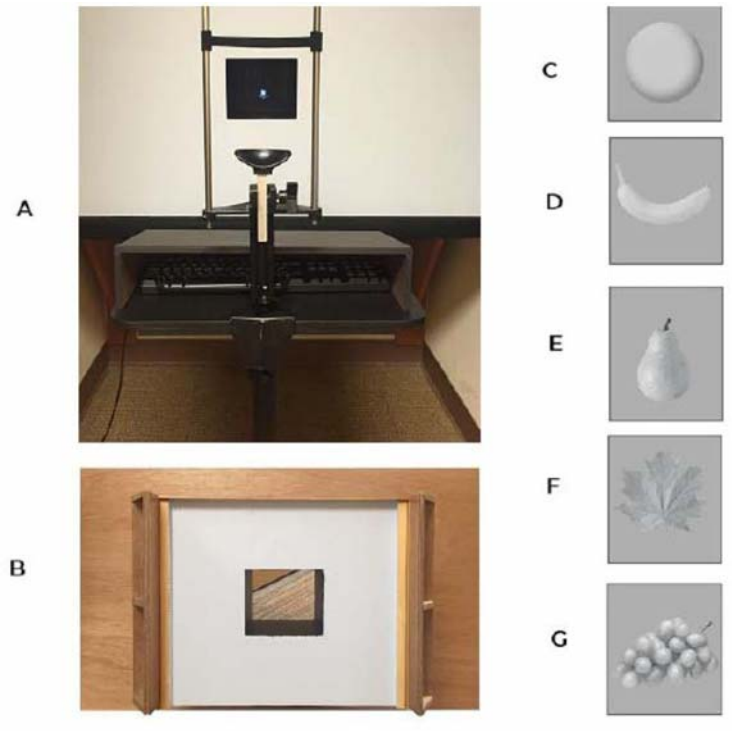

Figure 2. Photograph of the apparatus and stimuli (resized for viewing purposes) used in the present study. (A) trichromat's view during the experiment; (B) the dorsal view of the viewing tunnel which was firmly placed on the front of the CRT; (C) example of a circular disc; (D) banana; (E) pear; (F) foliage; (G) grapes.

Stimuli & Procedure

In each trial of part 1 of the experiment, each trichromat observed a homogenously coloured circular disc (3×3°). This object was carefully selected as it is an object which approximates real-world objects to a lesser degree. The luminance of the disc was set to 30 cd/m^2 while the background was set to 28.632 cd/m^2 in order to avoid any colour blending strategies [17]. The circular disc appeared with a tinted shade of colour chosen randomly from within the DKL colour space at a radius of 0.10 (10% of the maximum saturation allowed in the DKL colour space). The shade was created by digitally manipulating the pixels of each object (see Figure 3) 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 trichromat became less certain about the illuminant source and consequently the achromaticity of the object [18,19]. Note that the colour space used to define the stimuli in the experiment reported here is modeled after the second stage of colour perception, thereby reflecting the preferences of neurons in the Lateral Geniculate Nuclei (LGN) non-human trichromats (rhesus macaques) [20,21]. Furthermore, the trichromats' task was to adjust the hue of the disc until it appeared void of any hue. Adjustments were made by the keypress, along the isoluminant L–M (reddish-greenish) colour opponent axis, using the left arrow and right arrow, or along the isoluminant S–(L+M) (bluish-yellowish) axis, using the up and down arrows. Trichromats 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 trichromat got lost within the colour space, he or she could press the 'q' key, resetting the object to the initial colour 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 [15,17]. While there were no time constraints on the adjustments, the adjustment time was recorded. In the event a given trichromat pressed the "q" button the adjustment time wast set back to its initial starting point.

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 natural fruit objects captured under real-world conditions, instead of a circular disc. The banana was subtended 6.20° × 4.07°, the grapes, and the foliage was subtended 4.66° × 4.57° and the pear was 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). Secondly, in other to intensify the uncertainty of the illuminant source, 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 a canonical, deuterocanonical or opponent hue associated with the object. This was done by digitally manipulating the pixels of each object at a saturation level of 10%. In the 'canonical' condition, an object appeared with a tint of a canonical hue (e.g. purplish tint in the case of grapes, see Figure 3B). In the 'deuterocanonical' condition, an object appeared in a tint of a hue of a secondary association (e.g. yellowish for a pear). In the 'opponent' condition, the object was tinted with a hue situated in the opponent direction from its canonical association (e.g. blueish in the case of a banana). Although I call them 'part 1' and 'part 2' their order was counterbalanced in practice across trichromats. To maximize the reliability of mean chromatic adjustment value, each trichromat completed a total of 8 trials in part 1 and 80 trials in part 2 (equally distributed across objects and conditions).

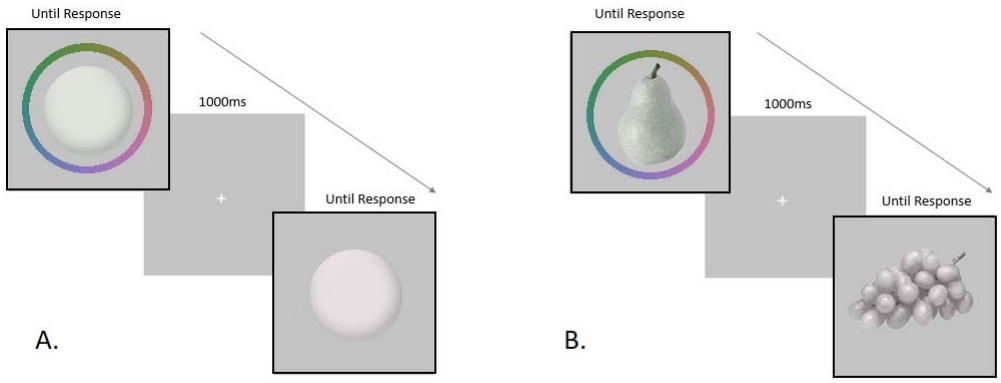

Figure 3. General procedure for part 1 and part 2: (A) circular disc, (B) natural fruit objects tinted in a greenish or purplish hue in order to create a shadow-like casting on the surface of the object. The colour ring (for illustration purposes) around the first trial denotes the possible colours within the DKL color space trichromats could adjust the

surface of the object to. The 1000ms fixation window which follows each trial was intended to control for any afterimage effect following the offset of each trial. The next trial without the color ring is a more accurate representation of what each human trichromat actually saw at the onset of each trial.

Results

Part 1 – circular disc

Using the horizontal meridian as the chromatic boundary to examine whether two types of groups 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 trichromat's mean chromatic adjustment was computed in part 1 across all trials. Shown in Figure 4A, the chromatic mean (blue diamond) revealed that 14 (females=9, males=5) out of the 25 trichromats adjusted the circular disc towards the S (bluish) pole 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 trichromats 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 (females =6, males =5) trichromats, the mean chromatic adjustments (yellow diamond) shown in Figure 4B, were biased towards the L+M (yellowish) 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.

Part 2 – natural fruit objects

In the natural fruit conditions – part 2, similar to my observation in part 1, the mean chromatic adjustments showed two distinct patterns, those whose chromatic adjustments were biased towards the yellowish pole of the S–(L+M) opponent axis and those whose chromatic adjustments were trending towards the bluish pole of the S–(L+M) opponent axis. What is of particular interest is that trichromats, to varying degrees, systematically adjusted the chromaticity for these objects towards the opponent direction of their mean chromatic locus in part 1. Specifically, for those whose mean chromatic adjustments were biased towards the bluish pole of the S–(L + M) opponent axis in the case of the disc, for natural fruit objects – irrespective of the canonical, deuterocanonical or opponent hue in which they were tinted – average chromatic adjustments were projected towards the yellowish pole of the S–(L+M) opponent axis (see Figure 4A, yellow square). The mean chromatic adjustments across all objects along the x-axis was with SEM of 0.0099, while the mean chromatic adjustments along the y-axis was 0.0384 with SEM of 0.0131. For the group of trichromats whose mean chromatic adjustments was projected towards the L+M pole in part 1, adjustments for the natural fruit objects trended towards the opponent direction, that is, towards the S pole (see Figure 4B, blue square). Across all trichromats, the mean chromatic adjustments 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.

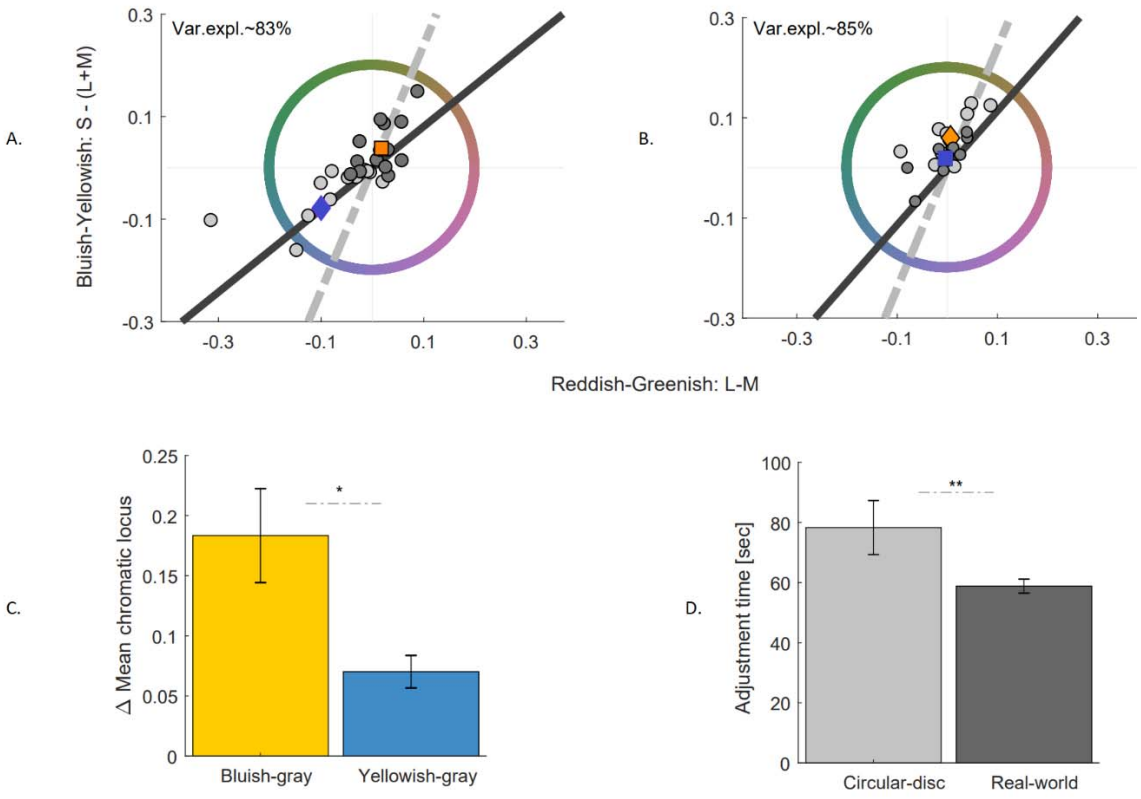

Figure 4. (A)Mean chromatic adjustments for the circular disc and natural fruit objects for group 1(n=14). (B)Mean chromatic adjustments for the circular disc and natural fruit objects for group 2(n=11). Light gray circle denotes the mean chromatic adjustments of the disc for each trichromat within each group, while the dark gray circle denotes the mean chromatic adjustments of the fruit objects. Mean chromatic adjustments across trichromats in each group for the disc and fruit objects is denoted with a diamond and square symbol respectively, while the filled color for each symbol indicates the color in DKL color space the mean chromaticity is trending towards. The black solid line is the 1st principal component axis, and the dotted gray line denotes the daylight axis. (C) Change, in Euclidian units, the mean chromaticity between the disc and the fruit objects for group 1 (yellow bar) and group 2 (blue bar) with their associated standard error of the mean. (D) Adjustment time across groups for the disc (light gray bar) and natural fruits (dark gray bar) with their associated SEM.

<u>Variation along the S–(L+M) axis</u>

For each group, in order to assess whether part 1 and part 2 chromatic adjustments covaries along the S–(L+M) opponent axis, and to what extent adjustments were distributed along the daylight axis (gray dotted line), a principal component analysis (PCA) was performed [22]. For the first group, the primary principal component axis explained 83% of the observed variance, while the direction of the main covariation was primarily projected along the S–(L+M) opponent axis. For the second group, 85% of the variance is explained by the primary principal component axis, which was also projected along the S–(L+M) opponent axis. For both groups, the principal component axis aligned much better with the daylight axis along the L+M pole of the S–(L+M) opponent axis in comparison to the chromatic adjustments around the S pole.

Difference in distributions between objects

To investigate whether the chromatic distribution within group is statistically significant between the disc and natural fruit objects, a two-sample Kolmogorov-Smirnov test was performed [23]. For the difference between the first group, distributions along the x and y-axis for part 2 was significantly different from normality, that is, the distribution observed in part 1 (x-axis and y-axis, $p<0.01$). For the second group however, the distribution in part 2 was not significantly different from normality (x-axis, $p= 0.7358$ and y-axis, $p=0.1473$).

Spatial and temporal dynamics

Chromatic displacement for each trichromat was computed by taking the Euclidean distance between the mean chromatic adjustment in part 2 from the mean chromatic adjustment in part 1. Following this, the mean chromatic displacement across trichromats within each group was computed (see Figure 4C).
For the group whose mean was projected towards the S pole, an average displacement of 0.183 (SEM=0.03) towards the L+M pole was observed. As it is expected for the second group, a much more modest chromatic displacement of 0.070 (SEM=0.01) towards the S pole was observed. A t-test was conducted which confirmed that the observed difference between the two groups was significant ($p <0.05$). To assess the temporal dynamics which accompanied the observed chromatic displacement, the mean adjustment time across each group for the circular disc and natural fruit objects was computed. Surprisingly a temporal difference was observed. Specifically, results show that for the circular disc, trichromats on average took 78.30 secs (SEM=8.99) to adjust the surface of these class of objects. Inversely, a much lesser time - 58.82 secs (SEM=2.32) was required for the natural fruit objects. A t-test was performed, which confirmed the significance of this difference with $p<0.01$.

Discussion

The hallmark of any dynamic system lies in its ability to rapidly modify its most basic architecture in response to external demands. 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, particularly in the cases when the core set of implicit assumptions and inferences the visual system typically relies upon become ill-equipped. While more recent studies have suggested that the human visual system deals with these cases by recruiting strictly one of two illumination priors – *PriorS* or *PriorL+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 either both types of priors or completely rely on a different set of implicit assumptions.

In part 1 of the experiment conducted, trichromats systemically adjusted the surface of the circular disc either towards the S or L+M pole along the S–(L+M) axis, which daylight is known to vary along. 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 visual system as to the chromatic property of the illuminant source it is to quickly discount[10,11]. Secondly, these results are also consistent with previous studies which show that trichromats typically fall into two distinct groups – blue and yellow group under these conditions. In part 2, for the trichromats who exhibited a particular bias towards the S pole for the circular disc, a significant opponent bias for the natural fruit objects was observed, while trichromats who exhibited a particular bias towards the L+M pole for the circular disc demonstrated modest opponent effects for the natural fruit objects. Prima facie these results appear to suggest that the visual system is in fact able to switch between both types of prior and that such plasticity is dependent on the type of object the visual system is attempting to stabilize.

However, this explanation does not hold if the modest effects observed for the second group is considered. To this end, it appears that the convergence in perception across trichromats for the natural fruit objects is due to what I have termed "spectral memory", the visual system's ability to actively record and update information, not about the color of the surface or the object (i.e. color memory and memory color) , but the spectral composition of the illuminant source, which a given class of object is typically illuminated under, information which is swiftly activated under poorly illuminated conditions, as it is reflected in the chromatic adjustments for the natural fruit objects measured in the experiments reported here. This is a particularly plausible explanation if we consider (i) the fact that most artificial illuminant sources are typically biased towards long-wavelength of light (i.e. the L+M pole) and (ii) classic electrophysiological studies in rhesus macaques in which spectral-specific neurons have been observed in the visual cortices [9,24,25,26]. Additionally, adjustment time results seem to suggest that when the operation guided by "spectral memory" is recruited, the visual system is able to stabilize the chromaticity of the retinal image quickly and more accurately when compared to instances when either PriorS or PriorL+M is being recruited.

To assess the validity of this idea, future studies on the psychophysical and neural domain should focus on how dynamic this spectral representation is, and whether the trichromatic system is capable of possessing different types of "spectral memory" for different classes of objects. For example, one way to test this idea

is to measure the representational differences between objects which are typically observed under natural illumination (e.g. personal car) versus those typically observed under artificial illumination (e.g. office desk). In this case, one would expect two distinct types of "spectral memory", which should be consistent with the spectral composition those objects are typically observed under. An even more intriguing way to test this idea is to measure humans across different age groups. Assuming that "spectral memory" works in the same way as spatial memory for example, which is known to be less reliable in older adults compared with younger adults, a difference in chromatic performance comparable to those observed in the spatial memory domain could possibly be observed [27]. In all, the stimulus composition and the chromatic adjustment procedure developed for this 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 modulatory effects on proximal retinal image.

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