Art, interpersonal comparisons of color experience, and potential tetrachromacy

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Abstract

Artistic representation of naturalistic scenes makes use of a range of visual processing features, and color and illumination are two that are frequently employed as strong dimensional emphases, especially in the medium of painting. Variations in human retinal photopigment classes are known to effect perception of light and color, and produce color appearance processing differences across individuals. We empirically investigated color perception in genotyped individuals with a potential for greater than three retinal photopigment classes compared to controls. We investigate both professional artists and non-artist participants using psychophysical designs that employed low-level motion processing of isoluminant color stimuli. Psychophysical results are used to design image-processing filters to identify components of visual scenes processed differently by potential tetrachromat observers. One filter converts values of psychophysically observed differences into a color scale, providing a first-order approximation of how inter-observer variation may impact spatial and chromatic features of natural scene processing. These simulations provide informative visualizations, across a range of scenes, allowing a normal trichromat observer to note specific portions of visual scenes that a potential tetrachromat observer may uniquely experience, and, suggest what portions of a scene a potential tetrachromat artist may be expected to paint in a uniquely artistic manner.

1. Introduction

Color, like many sensations we experience, does not represent an immutable feature of objects in the world. Color, very simply, is not in the world, and as such is not a genuine, or invariant, code or label that alone objectively identifies the state of the physical world when an observer is unavailable to process it, and color does not "belong" to observed objects. Rather color is a product of the minds of the world's observers, belonging to transitory states of the observers of objects. The composition of environmental illumination, the surrounding ambient context it is viewed in, subtle changes in an object's surface texture that alter an object's reflectance properties, and composition of natural scenes, are some factors external to an observer that contribute to color sensations. Internal factors that contribute to color sensations include visual processing system structural biology, internal mental state (e.g., levels of adaptation, awareness, chemistry) and visual processing experience. Most human observers asked to report what they see when they look out over a field of sunflowers will similarly describe colors experienced, "I see *yellow* flowers… *blue* sky… *dark brown* earth…," plus other visual qualities of the scene. The highly salient colors reported reside inside the observers' minds as individualized constructions of each observer's visual apparatus and the specific ways it translates visual information received from the world that are necessarily nonequivalent, yet observers' private sensory experiences seem consistent enough to maintain the contrary illusion, that we all perceive color in exactly the same way.

True, for the most part, even substantial changes in an object's color are, for practical purposes, discounted by human observers. [1] That is, we realize that color differences experienced for a particular sunflower when viewed in a sunlit field, compared to when that same sunflower is viewed in a vase on the kitchen countertop, should not be occasion for surprise or somehow interpreted as a different sunflower. But, nevertheless, the different sensations that arise from two such physical instances of color (that due to color constancy mechanisms, we cognitively process as "the same") are purely a product of one's individual manifestation of human visual processing biology.

Despite the highly personal nature of color experience just mentioned, several constraints on color perception, such as the absence of retinal photoreceptor classes, are well-understood. Thus, it is known that observers who lack (or have an anomalous form of) the class of long (L-) wavelength sensitive receptors are likely to experience color uncertainties in the span of hues ranging from yellow to green and through red.

Figure 1's two versions of "Sunflowers" by Vincent Van Gogh (who some speculate was color anomalous due to his occasional garish use of color) suggest subtle ways color appearance might vary as a function of protanomaly — a known color vision variation. Figure 1's image of Van Gogh's original painting on the left might appear to have an unrealistic amount of red pigment in the circular portion of the sunflowers, whereas the simulated protanomal view of the original painting (at right) shows that red is minimized considerably and green is less distinct. The protanomal view at right might be considered a more realistic and pleasant color composition for the painting.[1] And, if in fact Van Gogh was viewing the world through his own protanomalous filters while using his artistic skill to veridically represent his visual world, then Van Gogh's view of *both* the painting and the subject would resemble the version at right,[2] where the simulation conveys to non-deficient observers the internal aesthetic experienced and intended by the artist. The present study examines how such aesthetics are translated across observers when color perception experiences vary.

Figure 1. Original painting "Sunflowers" by Vincent Van Gogh (at left) and an altered version (at right) simulating the appearance of the original painting by an observer with Protanomalous perception [2]. Reproduced with permission.

2. Photopigment opsin genes and perception

The biological basis of color vision in all people begins with the photopigment opsin genes. Some individuals (most likely female) inherit genotypes permitting an extra class of retinal photoreceptor compared to the usual 3 classes of normal photopigments.[3] Typically individuals have genes allowing expression of three classes of retinal photopigment classes, and, although normal photopigment variation occurs, all trichromats presumably share a similar organization of color vision mechanisms even though not all trichromat observers have the same color appearance space.

While it is accepted that a trichromat's 3 cone classes enlist opponent process mechanisms and contribute to luminance contrast mechanisms, it is somewhat unclear how signals from an extra photopigment might be integrated into the neural color code in individuals possessing four distinct classes of retinal photopigments. We refer to individuals with retinas that contain more than the usual three photosensitive pigment classes as potential tetrachromats.[3,4] It is thought that potential tetrachromat individuals can express more than one class of long-(L) wavelength-sensitive cones [4-6] and, similar to normal trichromats, likely exhibit skewed proportions of one cone class type relative to another. In such individuals it is expected that they should express the standard trichromat opponent process mechanisms and luminance contrast mechanisms, but it is unknown whether signals generated four distinct photopigment classes might form novel opponencies that could impact color perception, or if the extra signals simply do not matter.

Although the prospect of human tetrachromacy is difficult to demonstrate empirically, the expectation is that this kind of X-chromosome-linked variant of the usual human color vision phenotype simply adds further variation to the possible configurations found in normal color vision individuals, and is useful for demonstrating how "normal" color perception is a personal construction that depends on both biology and experience. Evidence exists suggesting that women with a genetic potential for tetrachromacy exhibit an enriched color sense compared to a much larger segment of the population who have only three classes of normal cone photopigments. [5, 4, 7-11] However, whether the color vision of individuals with the genetic potential for tetrachromacy differs from that of a normal trichromat remains controversial. Standardized color vision assessment methods are inherently limited as human tetrachromacy detectors due to their optimization for distinguishing color deficiency from normal trichromatic vision. For these reasons novel methods for assessing potential tetrachromacy are needed.

The aim of much of the research into potential human tetrachromacy is to discover (a) how the possession of extra photopigment opsin genes may alter perceptual processing of color, and (b) what the X-chromosome linked features of the L-cone, and possibly M-cone, opsin genes imply for potential human tetrachromacy and gender-linked color vision processing differences.

We report investigations on these questions, and analyze what the findings imply for the use of color in artistic expression. We aim to: (i) highlight challenges inherent in communicating interpersonal comparisons of color experience. (ii) Develop and assess alternative methods for investigating aspects of color appearance linked to the addition of a cone class. And (iii) evaluate art work produced by potential tetrachromat individuals to explore whether such artists communicate features of tetrachromatic color experience through their paintings.

Here we compare potential tetrachromat color perception to that of normal trichromat controls. We discuss two factors contributing to color perception variation. (1) The genetic basis for normal human color perception that is known to vary across individuals, and (2) the idea that color perception might be trained up and enriched by early developmental experience and perhaps enhanced by prolonged exposure and cognitive manipulation of color across the lifespan. [11,9]

A. Photopigment opsin genotyping

As previously shown [4-7, 9,10,13] molecular genetics research has determined that genotypes involving more than three normal photopigment opsin variants are not uncommon, and that mechanisms governing expression of such photopigment opsin genes does not rule out the possibility that an individual will express more than three classes of retinal photopigments. The aim of much of the research into potential human tetrachromacy is to discover (a) how the possession of extra photopigment opsin genes may alter perceptual processing of color, and (b) what the X-chromosome linked features of the L-cone and M-cone opsin genes implies for potential human tetrachromacy and gender-linked color vision processing differences.

B. Participants

Six females volunteered for participation in an opsin genotyping study. For all but one subject (JK), photopigment opsin genotyping was performed after psychophysical assessment in the M-M isoluminance investigations (described below). JK's genotype was previously reported [4,7] and confirmed by the present genotyping study as reported in Table 1. All participants were genotyped using a novel implementation of genotyping methods described elsewhere. [6, 14] Figure 2 illustrates L-opsin Exon 3 Ser-180-Ala genetic sequence excerpts for two of the 6 participants found to exhibit potential tetrachromat genotypes. Table 1 provides identifiers for all female participant (col. 1); age at time of testing (col. 2); X-chromosome linked photopigment
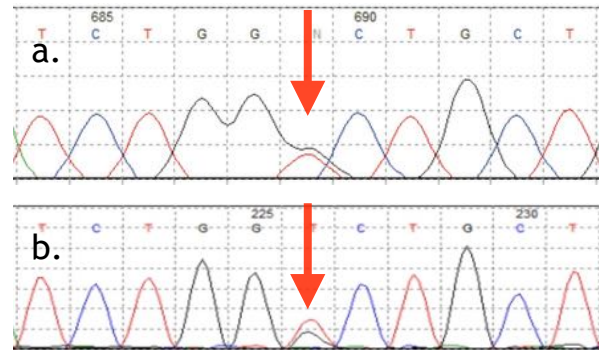

Figure 2. Genetic sequences (L-opsin gene, Exon 3, codon 180) for two different potential tetrachromat participants. Panel (a) and (b) respectively show CA and JK with different L-opsin gene codon 180 polymorphism. JK was additionally found to possess an M-opsin gene polymorphism (not shown). Curved peaks depict the intensity of the nucleotides (ddNTPs) observed in the DNA. Red arrows emphasize where serine and alanine polymorphisms are found.

opsin alleles (col. 3) detected for the L-opsin gene at codon-180 (Ser=serine, Ala=alanine, Ser+Ala=both alleles detected); reported presence of familial color vision deficiency (col. 4); presumed number of cone classes present in expressed phenotypes (col. 5); and reported history of art training beginning in early childhood (from 7 years). All genotyping investigations were performed with participants' informed written consent. Procedures adhered to protocols based upon the world medical association declaration of Helsinki ethical principles for research involving human subjects, and were approved by the ethical review board of the University of California, Irvine. Genotyping results are described below, followed by a description of M-M isoluminance investigations.

C. Genotyping results summary

Results in Table 1, col. 3, show, for each participant,

genotyping specific for a locus on the L-opsin gene that is known to be correlated with variations in color vision phenotypes. Two participants (AW and TC) were found to have two variants trichromat genotypes (M- and S-opsin genotyping results not shown). AW was found to have a normal trichromat genotype with a Serine allele at codon-180 of the L-opsin gene. TW was found to have an anomalous trichromat genotype with Alanine at codon-180 of the L-opsin gene.

Four participants (JK, CA, LA, LG) were found to have L- opsin codon180 heterozygosities thereby possessing potential tetrachromat genotypes. CA and JK exhibit different genetic sequences both of which provide the genes necessary for human tetrachromacy. Figure 2 shows L-180 allelic variants detected for CA and JK. Note, CA's genotype was previously assessed by an independent laboratory, and while uncertainty existed concerning CA's specific genotype, prior to the present genotyping CA she seemed a strong candidate for a potential tetrachromat genotype. JK's genotype was also previously analyzed and reported to have codon 180 polymorphisms on both L-opsin and M-opsin genes. [4, 7] and verified by the present repeat testing. Because genetic expression mechanisms a believed to rule out the expression of more than one M-cone class by JK, given theoretical assumptions, CA and JK are both considered Exon 3 codon 180 L- opsin gene heterozygotes.

Participants LA and LG also possess potential tetrachromat genotypes. LA is a female sibling of CA, whereas LG was a university affiliate. Discussion of LA and LG genotype results is reserved to Section 6. Section 3 below reports a preliminary psychophysical case study of color perception in potential tetrachromat artist relative to normal trichromat controls.

Participants detailed below include potential tetrachromat artist, CA, whose results are compared to those from:
(1) professional artist (TC) who is a trichromat with no known family color vision anomalies;
(2) a color vision "normal" female (JK), who has evidence of maternal family color vision deficiency, and has a potential tetrachromat genotype, and is not an artist,; And
(3) a color vision normal trichromat female (AW), with no familial color vision anomalies, and no artistic training.

3. Using Minimum Motion to investigate influences of photopigment genotype variations on perception

Analogous to effects used in the motion picture industry where a series of successively flickered static-image frames produce the seamless perception of a scene in motion, psychophysically created apparent motion is a dramatic form of illusory motion that is perceived when a series of stationary off-set image stimuli of *different subjective brightnesses* are rapidly presented, or flickered successively, across time. By comparison, when flickered stimuli are instead *subjectively equal in brightness*

Table 1. Six female participants studied.

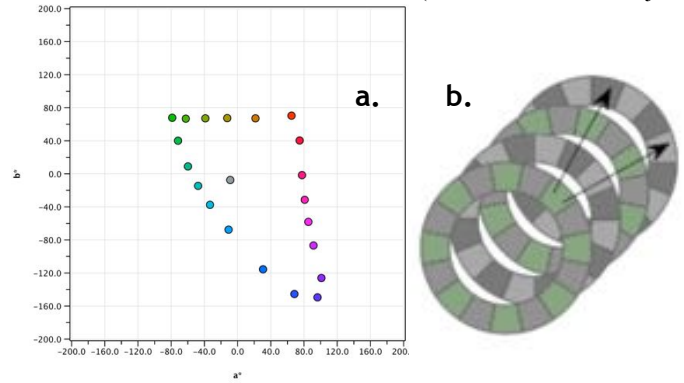| ID	Age	L-180 genes	Family CVD	Retinal cone classes	Artistic training
CA	53	Ser+Ala	yes	4	yes
JK	52	Ser+Ala	yes	4	no
AW	35	Ser	no	3	no
TC	70	Ala	no	3	yes
LA	51	Ser+Ala	yes	4	yes
LG	28	Ser+Ala	yes	4	yes

(in the stimulus format just

Figure 3. (a) Twenty hue stimuli tested in the M-M task plotted in CIELAB L(a*,b*) for the measured adaptation gray luminance level approximating L= 30 cd/m2. (b) Schematic of two predicted directions of perceived illusory motion in the M-M task for one of the 20 chromatic appearances tested. The four annuli shown depict rapidly presented sequential stimulus frames. The leftmost(rightmost) arrow indicates a "dark(bright)" match. Apparent counterclockwise(clockwise) motion occurs when the green patches are perceived as darker(brighter) than the adjacent mid-level gray patches.

described), the illusory motion is instead "ambiguous" and reported with essentially equal frequency as moving in one direction or the other. Such "Minimum-Motion (M-M) isoluminance settings" vary greatly across individuals [15] and are not expected to be uniform across perceptual color space. The visual system is sensitive to very small amounts of luminance differences in this task, that when optimized appropriately yield highly reliable, accurate estimates of an observer's personal settings of subjective isoluminance [16]. As such, the M-M task is a commonly used isoluminance calibration procedure used to obtain individualized color settings with which to define isoluminant color stimuli in a subsequent task. The paradigm was recently used to behaviorally classify individual differences in retinal physiology underlying perceptual variability among observers due to a double dissociation between minimally-saturated red and green, and spatial frequency [17,18], and extending this finding, to model non-uniformities in individuals' isoluminant planes [8], which was used in the current study and described later.

In general, isoluminance estimates obtained using hue and spatial frequency variation are likely to be depend on various factors including the relative number of L:M cones expressed in an individual's retina, peak photopigment sensitivities, and number of distinct cone types. This being the case, normal color vision observers may be expected to have different M-M isoluminant settings compared to observers who have the potential for tetrachromacy.

If comparing isoluminant settings across a given observer's perceptual color space informs us about the contributions made by that individual's different photoreceptor classes, then we suggest that comparing settings of isoluminance *across individuals* may further tell us something about the ways settings may vary due to signal processing arising from retinas with three versus four photoreceptor classes.

A. Empirical rationale

Use of the M-M design here is exploratory, and to our knowledge M-M isoluminance has not previously been employed to investigate color processing among opsin genotype variants. It is used here because: (a) It provides an alternative to existing color vision assessment methods which are not explicitly designed to reliably detect color vision differences that might arise from retinal
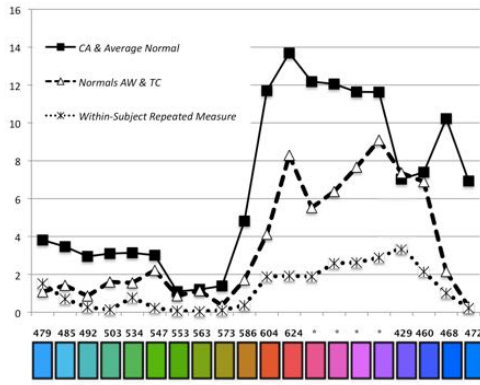
Figure 4. Three curves show observed differences relative to RGB display primary units found for M-M isoluminance settings comparing 4 participants. Y-axis gives magnitude (in RGB Euclidean distances) of differences between two participants' observed M-M settings. X-axis shows approximations of 20 stimulus conditions used and measured dominant wavelength in nanometers (conditions with two dominant wavelengths are denoted with an "*" value).
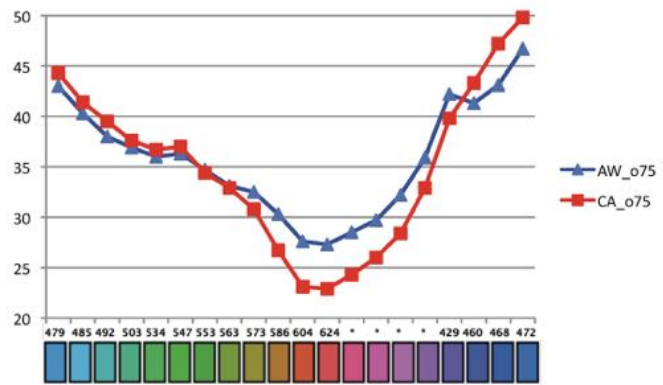

Figure 5. Luminance measurements of M-M isoluminance settings for CA (red line) compared to normal trichromat AW (blue line). Y-axis shows cd/m^2 measurements. X-axis depicts the 20 stimulus conditions used and their measured dominant wavelength in nanometers (conditions with two dominant wavelengths "*" as values).

tetrachromacy.[4,6,7] And (b) it permits testing judgments for luminance, color and motion in a context.

The latter seemed an important empirical consideration because, point of fact, color sensations evolved under naturalistic viewing, in complex visual contexts, including moving dynamic scenes, and context provided by foliage and forest canopies, under illumination changes, and rarely as isolated color patches. For this reason, we adopted manipulations of viewing complexity that might facilitate differentiation of potential tetrachromat CA from trichromat controls. We did this because overly simple, non-naturalistic, viewing circumstances may not be complex enough to enlist nuanced contributions to color processing that may be contributed by an extra class of photoreceptors that a potential tetrachromat possesses.

Following this reasoning we tested CA using a variety of contexts such as personally constructed luminance and chromatic variations of adaptation state. For example, in addition to a neutral gray, we incorporated a chromatic background (at a chromaticity that optimized CA's presumed photoreceptor responsivity) as an adaptation background variant. We also investigated low luminance levels based on promising indications from pilot investigations. Consideration was also given to uses of color found in the art work of the potential tetrachromat (e.g., detailed in the discussion below). The aim of all manipulations was to increase the chance of detecting a tetrachromat processing difference where one existed.

To explore these possibilities we psychophysically evaluated the individual settings of subjectively equivalent "brightness" in a M-M task for the 20 hues (approximated in Figure 2a) for two potential tetrachromats and two trichromat controls. As Exon 3 codon 180 L-opsin heterozygotes, CA and JK have the potential to

phenotypically express four distinct photopigment classes in their retinas. Part of the present investigation sought to devise a reliable psychophysical method for behaviorally identifying retinal tetrachromat phenotypes.

We employed a well-established, highly reliable "Minimum Motion" (M-M) paradigm.[15,16] Experimental apparatus, stimuli and procedures used are based on the accumulated work of Herrera, Winkler, Chubb, Sperling and colleagues.[17-19] The paradigm was recently used to behaviorally classify individual differences in retinal physiology underlying perceptual variability among observers due to a double dissociation between wavelength and spatial frequency of stimuli used. [17,18] Herrera [19] expanded the color conditions explored from the minimally-saturated red and green (used by Winkler and colleagues) to twenty color conditions consisting of maximally-saturated hues from a color space isoluminant plane. The present M-M investigations used the design of Herrera [19]. We use this paradigm to obtain participants' personal settings of subjectively equivalent "brightness" in a M-M task for 20 color conditions. Such settings are 20 highly reliable points where individual's isoluminance adjustments establish a minimum illusory motion percept attributable to subjective brightness differences between constant gray patches and 20 separately defined color patches. Table 2 summarizes the design involving seven experiments under four adaptation luminance levels and two background contexts.

B. Methods

Subjects and Design. Phase 1 involved 1-2 hours of testing to assess color vision using standardized methods. Phase 2 involved testing, over several sessions, seven M-M isoluminance experiments (~40-50 minute duration). Total approximate duration of experimental participation is estimated at between 5.5 and 7.5 hours, distributed across several days. All M-M investigations were performed with participants' informed written consent. Procedures adhered to protocols based upon the world medical association declaration of Helsinki ethical principles for research involving human subjects, and were approved by the ethical review board of the University of California, Irvine.

Phase 1: Participants were assessed using standardized procedures and some novel analysis approaches. Diagnostics for color deficiency used were Ishihara Pseudo-isochromatic Plates, the Farnsworth-Munsell 100-hue Test, and (for participants CA, AW, TC, and JK only) the O.S.C.A.R. flicker photometric test

Table 2. Seven M-M isoluminance experiments.

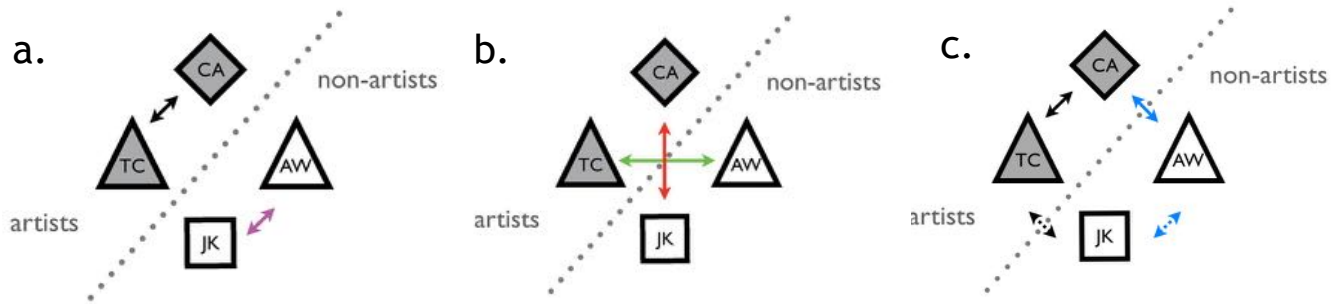| Adaptation Level	Uniform Neutral Gray Background	Uniform Color Background
1. Lowest	20 colors; 50 trials each	20 colors; 50 trials each
2. Low-mid.	20 colors; 50 trials each	20 color; 50 trials each
3. High-mid.	20 colors; 50 trials each	20 colors; 50 trials each
4. Highest	20 colors; 50 trials each	not assessed

Figure 6. *Three modeling scenarios considered for four participants who vary with respect to (i) color vision genotypes, and (ii) perceptual learning due to early exposure to color through art training. Square symbols denote participants with a genetic potential for Tetrachromacy. Triangles are participants with trichromat color vision possessing trichromat genotypes. Shaded symbols depict trained artists. Unshaded symbols are individuals with no formal art training or explicit early color training experiences. Double arrows wedged between two symbols denote the comparative M-M differences considered in each panel.*

and the Neitz anomaloscope matching task.

Phase 2: Participants tested in seven M-M experiments. Subjects sat with restricted head movement to view a computer screen (~22 inches distant) and responded to M-M stimulus by key-press indicating direction (left or right) of perceived stimulus motion. Stimuli subtended 2.1 degrees of central visual angle, as a small spinning disk. Otherwise the display was chromatically uniform, at a specific luminance level, for a constant observer adaptation state. Figure 3(a) shows CIELAB coordinates of 20 color conditions tested, approximating one observer's final settings. Over seven experiments a subject provided ~7000 M-M judgments (plus practice and initiation trials). Table 2 lists trials per experiment. Results are presented for Table 2, row 1 experiments.

C. Results

All six Table 1 participants scored color vision normal on all color perception tests, measuring normal or above average performance using two standardized color vision diagnostics, Ishihara Pseudoisochromatic Plates and the Farnsworth-Munsell 100 hue test.

M-M analyses presented here investigate only if participants' measured isoluminant settings reveal differences in perceived brightness for the 20 color conditions that were tested, and whether any association is found between those differences and color vision genotype or evidence of art training and experience manipulating color materials across the lifespan.

Comparisons involve contrasting the M-M settings of CA with 3 female participants. As mentioned earlier, TC is a trichromat artist, AW is a trichromat non-artist, JK is a potential tetrachromat non-artist, possessing a combination of retinal photopigment genes that differ from CA's. The present M-M isoluminance task to involve an adaptation background color that is spectrally dominant near the peak response of CA's presumed extra photopigment class. Thus, the experiment is designed to test for (1) whether CA is more sensitive to subtle differences in a range of colors compared to control participants. And, if so, (2) whether CA's difference is due to (a) being an artist or (b) being a potential tetrachromat, or (c) necessarily being both (a) and (b).

Results Summary: Results found for tests (a) – (c) reveal that compared to control participants tested: (1) CA's differences were highly significant, but varied across conditions tested in all experiments; and (2) CA's potential tetrachromat differences were found most apparent in data under the (i) chromatic context (e.g., color background) experiments, (ii) experiments using lower background luminance levels, and (iii) for stimulus conditions dominant in "reddish" regions of color space.

Results unambiguously support conjecture (c) stated earlier: CA's differences are necessarily due to being both (a) an artist and (b) a potential tetrachromat.

Results detail: We quantify CA's potential tetrachromat effects by comparing CA's perceptions to that of control subjects tested. As a result, analyses here only report *potential tetrachromat performance differences relative to control performance.*

However, before analyzing potential tetrachromat effects we first quantified the degree of *normal difference* found between two color vision normal subjects.

Quantifying normal variation in M-M isoluminance settings: There is known variation in individual subjective isoluminance even among individuals with normal color vision. We compared two normal trichromat control females (AW with TC). In order to determine an appropriate baseline for further comparisons, we first calculated the mean unsigned T-value derived from paired t-tests between AW and TC across all twenty color conditions, and for each background tested. The mean degree of significance for the lowest-luminance gray condition (Mean = 6.86, SD = 7.9) was comparable to that of the lowest-luminance chromatic condition (Mean = 7.97, SD = 8.5). In order to meet our more conservative criterion, subsequent t-values were required to be greater in degree than our normal trichromat mean deviation plus one standard deviation (e.g. +/-14.76 in the gray condition and 16.43 in the chromatic condition). Since this more conservative criterion renders observed AW-versus-TC differences insignificant, results from all other comparisons between other participants were compared to an average normal trichromat (e.g., "Average Normal," ticked line with triangles, in Figure 4) defined by aggregating the data of two normal trichromats, AW and TC. This result, in conjunction with the earlier findings [8] provides a benchmark for evaluating what would be expected as normal individual variation among participants assessed.

Figures 4 and 5 plot a single condition tested where large individual differences in observed settings are indicative of results trends. Figure 4 plots three different pairwise comparisons between two sets of M-M settings (y-axis) for the 20 stimulus conditions tested (x-axis). Figure 4, top curve, shows participant CA differs most from an average trichromat control for settings involving "reddish" stimuli; the middle curve shows significantly less variation when comparing two normal trichromat controls (AW & TC); and the bottom curve shows minor baseline variation seen in one individual's (TC) repeated measure performance. Note, if observed, a graphed flat horizontal line at y-value=0 would be seen if no differences existed between two participants' compared settings. Curves shown here deviate from that zero-difference scenario, and illustrate the regions of color space where variation in participants' M-M setting were found, and the magnitude of those variations relative to the idea of a zero-difference baseline, and the average repeated-measure difference found for participant

TC (bottom curve). In sum, Figure 4 curves comparing participants' stimulus settings (in nonparametric digital display RGB values) show areas of large, atypical, variation and suggest that for some color regions, potential tetrachromat CA performs very differently from the other participants tested.

Figure 5 illustrates how spectroradiometric measures convey observed differences between CA (the artist) and AW (the non-artist normal trichromat), as differences in the two participant's settings in terms of measured luminance information present in color stimuli. In Figure 5, CA's important differences compared to trichromat AW are: Spectral regions showing (1) significantly different isoluminance settings, and (2) different patterns of observed isoluminance settings. Additional results suggest these differences are due to luminance processing, and imply that CA's extra photopigment class plays a crucial role in her M-M settings for the color space regions tested.

Based on these preliminary results comparing CA's M-M settings to normal trichromat control participants, we tentatively conclude: (1) Potential tetrachromat CA's exhibits (*i*) non-deficient color perception (E.g., excellent performance on standardized color vision tests), and (*ii*) M-M isoluminance settings that markedly differed in some regions of color space compared to normal trichromat controls. (2) the comparative sensitivity reflected in CA's M-M settings seems to suggest she is expressing a fourth cone class population (presumably a long-wavelength sensitive cone class variant) which is contributing to cues used in the M-M isoluminance task, in addition to the usual signal contributions arising from M-, L- and S-cones that normal trichromats possess. Both results are consistent with results that suggest individuals with potential tetrachromat genotypes exhibit richer color experience compared to trichromat controls.[4, 6]

These results suggest that potential tetrachromat CA: (1) Has color perception that is both non-deficient and non-normative. (2) Establishes minimum motion for some color stimuli at luminance levels that are outside the range of isoluminant settings found the normal trichromat controls to which she has been compared. (3) Exhibits settings for isoluminant, or equally bright, stimuli that show her greatest deviations from normal include stimuli with substantial mid- to long-wavelength, or "reddish", spectral components – a result consistent with the idea that she expresses a fourth cone class which is the basis for her setting differences compared to those of trichromatic controls. (4) Exhibits enriched color experience in dim light conditions (low photopic vision) such as in shadows and for low daylight levels. This last item (4) is also suggested by themes seen in CA's artwork, where a preoccupation with elements in shadow and low illumination are found (see Section 5 and 6 below).

4. Influences from artistic training

The idea has also been suggested that color perception may be *trained up* by early developmental experience and perhaps enhanced by prolonged exposure and frequent cognitive manipulation of color across the lifespan.[11] Is it the case, then that artistic training serves as a model for our observed M-M setting variations as well as the opsin genotype variation?

Figure 6 depicts three empirical questions, or models, that can be posed concerning the roles played by photopigment genotype-phenotype and artistic training, towards modeling Section 3's M-M isoluminance setting variations. That is, Figure 6, panel (a.) suggests a model where photopigment opsin genotype alone explains the comparative M-M settings of two observers with similar artistic training. Panel (b.) suggests a model wherein early exposure to art training explains the comparative differences seen in M-M settings of two observers of similar genotype (phenotype). And panel (c) suggests a model in which a combination of photopigment genotype and art training best captures comparative M-M settings of observers. In evaluating all three we used the greater-than-2-standard-deviations difference criterion for defining an observed potential tetrachromat settings difference relative to control settings. Using this criterion these 3 simple models are evaluated.

Figure 6(a)'s genotype/phenotype model assessment: Support for Figure 6(a)'s model is implied if both black and pink arrows represented statistically significant differences for the observed empirical settings of compared participants. Section 3's M-M results confirm that comparisons depicted by both black and pink arrows depicted in panel (a) were both significantly different - especially for "reddish" color stimulus conditions — a result seen in Figures 4 and 5. Figure 4 shows that potential tetrachromat CA differs most from an average trichromat control in conditions involving "reddish" stimuli; and Figure 5 illustrates setting differences between CA and normal trichromat AW are linked to luminance variation.

Figure 6(b)'s artistic training model assessment: Support for Figure 6(b)'s model is implied if both green and red arrows were statistically significant differences for the observed empirical settings of compared participants. Section 3's results find that comparisons depicted by green and red arrows in panel (b) were not both found to be significantly different. That is, the green arrow comparison, between AW and TC, was not different (by the 2 SD criterion). Thus, for this pair of trichromats Section 3 results imply either (i) early exposure to art training is not sufficient to predict the M-M setting differences of these two trichromats, or (ii) art training alone does not appear to be sufficient to predict the differences in M-M settings observed for these two trichromats (implying a different, more sensitive, test may be needed).

In contrast, panel (b)'s red arrow comparing tetrachromat genotypes was significantly different (by 2 SD). Thus, for this pair of putative tetrachromats, results suggest that early exposure to art training models M-M setting differences found for participants CA and JK. This latter finding is preliminary, however, since the present empirical task was designed to optimize photopigment sensitivities specific to CA, making the task more likely to detect CA's specific form of tetrachromatic potential compared to that of JK (who possesses a different and less straightforward potential tetrachromat genotype).

Preliminary findings for Figure 6(b)'s model are: (i) Early exposure to art training is not sufficient to predict the differences in behavior between the two trichromats AW and TC. And, (ii) for potential tetrachromat participants CA and JK, exposure to art training is a factor that predicts performance differences in this M-M task (although further assessment is needed).

Figure 6(c)'s combination model assessment: Support for Figure 6(c)'s model is implied if both (blue and black) solid arrows were significantly different at levels equal-to, or greater-than, the similarly colored dotted-arrow comparisons shown in panel (c). Results show that comparisons depicted by both blue and black solid arrows in panel (c) were observed to be different by a greater amount from the respective dotted arrow comparisons.

Thus, M-M results support the panel (c) model, suggesting that photopigment genotype/phenotype and early art training factors appear to synergize, and seem to contribute in an additive fashion to the amount of difference found between participants' M-M isoluminance settings.

Modeling results summary:
For all Figure 6 models assessed, observed variation between M-M settings was substantial for some compared pairs, and, variation was never uniform across all conditions or experiments. In general, M-M setting differences tended to be most

pronounced for (1) experiments involving a chromatic context (e.g., color background), (2) experiments using lower background luminance levels (i.e., ~30 cd/m^2 adaptation levels) and (3) for color stimuli with substantial energy components in spectral regions normally associated with "reddish" appearances.

These findings preliminarily establish that CA exhibits important differences from the tested trichromat controls. That is, CA exhibits (1) non-normative **levels** of M-M isoluminance settings, and (2) non-normative **patterns** of M-M isoluminance settings. These results suggest CA's differences are luminance based, implying her extra photopigment class is plays an important role in the M-M settings she established in color conditions assessed. Moreover, they unambiguously support the conjecture that *genotype/phenotype* and *early art training* factors synergize.
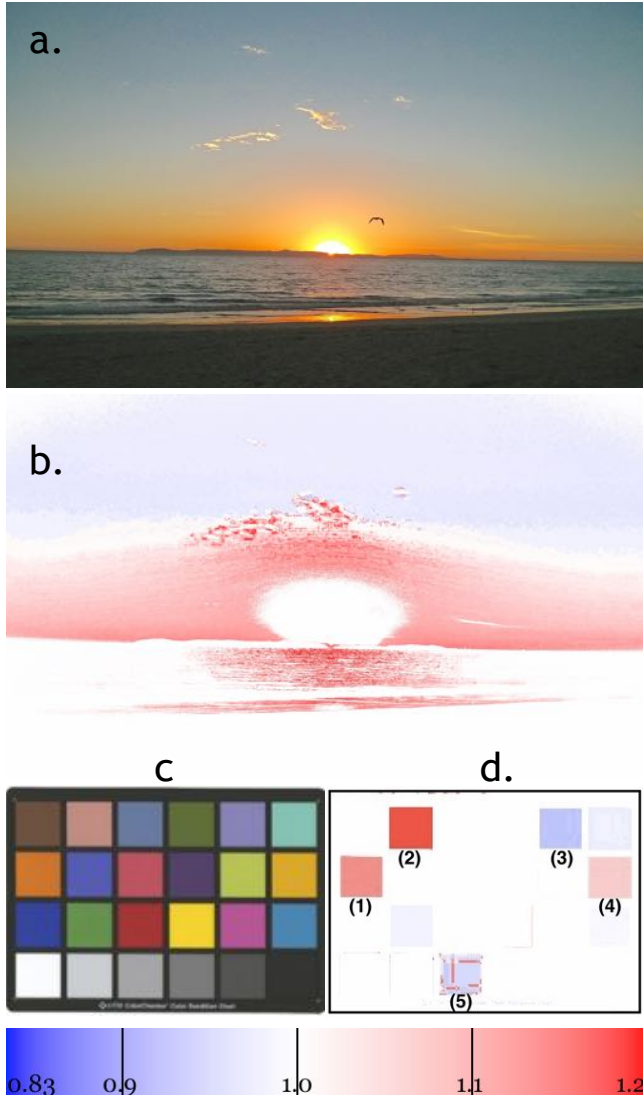

Figure 7. Toward representing phenomenological differences (a) Photographed sunset image. (b) Simulated image conversion statistics based on measured luminance settings for CA relative to those of normal trichromat control AW. CA and AW differ in the processing of the image shown for 66% of image pixels. Pixels perceived the "same" are white in this diagram, corresponding to a value of 1 on the heatmap scale shown at the bottom of the figure. Red pixels (ratio > 1) signify original image color values that (and the degree to which) CA's perception is "more sensitive" than a normal observer. connotes needing less wavelength-specific luminance energy to establish isoluminance relative to an adaptation field standard. Image pixels that are colorized as the heaviest blue are different by being less sensitive than what a normal observer would see (i.e., pixels needing more wavelength-specific luminance energy to establish isoluminance). (c) The Munsell Color Checker, a standard used in color reproduction science and industry. (d) Simulated image conversion of the Munsell Color Checker. At bottom, heatmap color scale used.

Figure 8. Representational plein aire art by potential tetrachromat CA. (a) Original oil "Canyon Cameo". (a) A photo of painting and subject. (b) The palette of color appearances (identified through completely separate analyses Section 3's independent data) clearly exaggerated in the painting in (a). Section 5(A.) methods empirically identified the palette in (b), similar to analyses in Figure 7(c & d). Image © Concetta Antico. www.concettaantico.com. Reproduced with permission.

Thus, CA's non-normative perception appears to be due to her being both an artist and a potential tetrachromat.

5. Simulating tetrachromat color perception

As we look out across a field of sunflowers, we typically have no reason to suspect we are not sharing the color experience of others. Given the protanomalous differences suggested in Figure 1, what kind of variation should be expected if an additional photoreceptor class were contributing to the perception of light and color in a visual scene?

If we agree Vincent Van Gogh's use of color is rich, like many fine artists, but includes lines of diverse color intermingled and places where entirely different colors are interjected, including some unusual uses of color. [2] This might lead us to surmise, as some have, that Van Gogh had a color vision deficiency. Noticing subtle color variations in Figure 1 is straightforward because for most normal color vision observers it is easy to both (a) imagine attenuated color experiences, and (b) visually appreciate simulated image changes achieved by specially designed anomalous trichromat or dichromat filters.

By comparison, it seems considerably more difficult for a color vision normal individual to imagine and appreciate experiences that might be conferred by a retinal tetrachromat's extra cone class. This could occur if tetrachromat processing used information from that extra source in ways that are not accessible to observers who lack signals from a fourth photoreceptor class. For these reasons it may be difficult for a tetrachromat to articulate their color experience to a trichromat, especially if they involve qualities outside those that trichromats regularly experience. And, it is essentially impossible to devise a way to allow a normal trichromat observer to "see" a natural scene as a human tetrachromat does (since a trichromat may not have access to some sensations and distinctions arising from an extra pigment class). Thus, while its fine to wonder how natural scene perception may differ for a potential tetrachromat, it's difficult to directly simulate.

As Figure 1 illustrates, one way to appreciate variation in color sensation across individuals is to analytically simulate observer perception using models of photopigment processing. This is easily done for color deficiency, and involves converting reflectance data from naturalistic images using known photoreceptor response information from observers with non-normative color vision. Here we aim to bridge the experiential gap between trichromats and potential tetrachromats by proposing a procedure for displaying relative scene processing differences between the two.

A. Method for converting photographic images based on individuals M-M isoluminance settings

Figure 7 provides one demonstration of scene processing by potential tetrachromat CA relative to trichromat participant AW. Briefly sketched, the method we designed for such conversions analyzes each pixel of an original photographed image (e.g., Figure 7(a).) and uses CA's empirically observed comparisons to AW to determine which pixels of the original image CA would experience differently from AW. We then convert each image pixel that would appear different to CA in quantifiable way, to a black pixel, and convert pixels that will not look different to white pixels (conversion not shown). The proportion of changed pixels varies from image to image (depending on properties of the original scene), but for Figure 7's sunset image a large number (~66%) of pixels are estimated to look different to CA compared to normal trichromat control AW. Also, for any image converted not all pixels are effected equally. Figure 7's image conversion can be expressed as a function that captures the magnitude and distribution of the estimated perceptual differences. Thus, pixels altered by an amount between 0 - 5% are 43.90% of the image pixels. Pixels altered by 5 - 10% are 11.20%. Pixels altered by > 10% are 10.93%. Total pixels changed are 66.03%.

Figure 7(b) takes the simulation one step further by refining the image information using a meaningful heatmap color code (the heat map scale used is Figure 7's the blue to red legend). To create panel (b) all image pixels first tagged as pixels of difference were changed to some color from the heat map range which varies from a strong red, through white, to a strong blue. The extremes of the heatmap continuum indicate the greatest differences between CA and AW. Between the extremes the color scale varies as a log function of %-boost experienced by CA relative to AW (where boost is a parameter given by a psychophysical function derived from spectral measures for hue and luminance (CIELhc) given pixel RGB values, and is therefore based entirely on the observed comparison of CA's empirical data with that of AW). Values at the red extreme of the scale indicate CA's data reflect an increment difference. Blue extreme values code for change by a decrement difference. Thus, in panel (b) pixels coded heavy red, can be understood as pixels that are seen differently by CA as being more "powerful" than what a color vision normal observer would perceive, whereas pixels coded as the heaviest blue are experienced by CA as less powerful, or less intense, compared to what our normal observer sees.

B. Filter-based analyses of artistic representation

Figure 7(d) shows the output from our conversion algorithm applied to the Munsell Color Checker (a colorimetric standard). Based on our relative comparison of data from CA with that of AW, we find that the modeled potential tetrachromat psychophysical transformation has the following properties:

(*i*.) It does not involve uniform variation from normal across all spectral frequencies — some frequencies are impacted more than others. For example, spectra of color tiles numbered (1) to (5) in Figure 7(d) are perceived differently by CA, whereas the other color tiles in the original color checker image (c) are not. (ii.) It's deviations from normal do not represent changes in a uniform

direction — that is, sensitivities for some colors are increased, whereas sensitivities for others are decreased. And, (iii.) It does not always deviate from normal — that is, for some spectral frequencies the tetrachromat psychophysical function processes stimuli in a manner that is statistically indistinguishable from normal processing.

These data suggest that while some processing differences may be very significant they are not global, and they do not always involve a heightening of perceptual processing. To our knowledge such subtleties have not been systematically described in previous empirical reports investigating the psychophysical functions underlying human potential tetrachromats. Also, color stimuli in Figure 7 (c) that are tagged by the algorithm are of interest qualitatively. Concentrating first on the Munsell Color Checker stimulus, two orange-ish samples (i.e., tagged as (1) and (4) in panel (d)) are stimuli closest to the peak wavelength area of CA's extra photopigment class, and are found to differ in a positive "boost" direction, which is consistent with the idea that her extra photopigment class is contributing to an isoluminance signal. The rose colored tile (labeled (2) in panel (d) is tagged for the greatest "boost" difference, and as a reddish-blue stimulus is perhaps a bit of a puzzler from the standpoint of our current modeling perspective – however, the present model is admittedly only a first-order approximation of possible scene processing differences. Last, there are lavender (labeled (3)) and gray (labeled (5)) stimuli that change the greatest in the scale's "anti-boost" direction. Thus, two bluish-reds (a rose with blue tint (i.e., (2)) and a lavender blue with some red in it (i.e., (3)) are the extremum coded by the heatmap scale. Note, mid-level gray stimulus (5) in panel (c) shows signs of a multivalued artifact – blue conversion code with red code aliasing – because the hue and luminance levels of the original gray stimulus straddle a tipping point in the algorithm.

Filter algorithms of this sort serve as a tool for objectively analyzing and inventorying the contents of both naturalistic scenes and their painted counterparts. Such analyses may lend insights on artistic hallmarks of tetrachromat artists' visual processing and artistic representation. Figure 8 shows a *plein aire* painting that by CA's self report *aims to represent what the artist sees*. Very apparent in Panel (a) is the use of additional color on the canvas that is not obvious in the photographed scene. Analyses suggests the extra color is not random. The artist is not simply adding extra color, of every sort, everywhere. Panel (a)'s additional colors systematically align with colors in panel (b) which M-M results indicate the artist has greater access to at lower light-levels compared to a normal observer. That is, CA is primarily adding color to the scene, especially in shadowed portions, from regions of color space independently found to be those for which she differed substantially from a normal control. Similar analyses can be made of CA's other works, and, in general, this approach permits preliminary evaluation of where M-M data suggest CA differs from a trichromat in natural scene interpretation.

Based on these results, CA seems to be painting her impression of the ambient light and its interplay with the scene. One could speculate that in Figures 8-11 CA appears to be communicating to her trichromat audience: "Look, I see this color and tone in these shadows, I see a range of tints in this sky, I see color contrast and veiling in the spaces adjacent to these surfaces." In other words, CA seems to be painting the effects of light in nature, using added color and color relationships. These informal studies suggest extra color in her paintings is not simply a stylistic interpretation that she adds for the benefit of her audience, it is her way of communicating her view of a natural scene, emphasizing color, that she realizes from experience, normal trichromats may not fully appreciate.

C. Comparison with trichromat art

It is important for Figure 6's modeling comparisons to establish that TC's artistic prowess compares to CA's. Consider

CA's the use of color in Figures 8-11 with the color use of trichromat control artist TC's, in Figures 12 and 13. TC's art also suggests a very high level of learned color expertise (making her an appropriate artist control participant), but CA's uses of color in her paintings appear to differ from trichromat participant TC's uses of color.

Depiction of rock formations in TC's art (Figures 12-13) show strong, astute use of color, emphases of color variation in surfaces. Trichromat artist TC is no slouch with respect to uses of color in representing surface reflectances. However, compared to artist CA, TC seems to use color in different, possibly in stylistic

Figure 9.. Original oil painting, "Tetrachromat Moon." © Concetta Antico. www.concettaantico.com. Reproduced with permission.

Figure 10. Original oil painting "The Eye Of Heaven." © Concetta Antico. www.concettaantico.com. Reproduced with permission.

Figure 11. Original oil painting "Midnight Super Moon" © Concetta Antico. www.concettaantico.com. Reproduced with permission.

ways that specifically accord with the palette of a color-vision normal viewing audience, as her painted shadows are deeper achromatic shades and deeper blues, highlights are contrasting yellows and higher lightness values, the result is beautiful, highly skilled, and engages the viewer in prolonged interpretation, but the *kinds of color* used -- the palette and the emphases -- seem to be trichromatic emphases, and there is little or none of the lavender, rose, orange and gold tinges that one finds in CA's shadow work. Thus, while trichromat artist TC shows very adept and complex color use in her painting, the uses do not seem to signal "*I see more, or different, color here …*" and, instead, color seems to be used for emphasis of contours, and contrasting color for dramatic or emotional effect, or to embolden a line or object. Such uses of color may follow more from a conceptual or dramatic technical contrast, rather than from an impressionistic rendering of observations of a scene as seems to be occurring in the examples by CA. These preliminary comparisons help convey how CA's artwork is very likely capturing signaling impacts on color perception that arise from an extra photopigment class. These works of art demonstrate that potential tetrachromat CA and trichromat TC are both color experts and exceptional painters. This fact coupled with the highly significant differences seen when comparing CA's and TC's empirical data suggest that art training is not the sole basis for CA's observed deviations from normal. CA's genetic potential has likely been trained up by her many years of extensive art practice, and these two factors seem to synergize and contribute to the unique color perception underlying her observed empirical differences.

6. Other potential tetrachromat artists

Table 1 gives information for two additional potential tetrachromat artists, namely LA and LG. It is important to note that prior to genotyping LA was considered a likely candidate for a potential tetrachromat genotype because she is the sister of CA. By comparison, LG was initially enlisted in the present investigations as she is a skilled amateur artist who was believed to possess a normal trichromat genotype. Subsequent genetic testing revealed that LG also possessed a potential tetrachromat genotype, and could not be used here as an artist trichromat control.

The art of both these potential tetrachromat artists is worthy of mention in the context of the present study. For example, Figure 15 works by LG illustrate a strong emphases of color in shadow as has be noted in the work of CA. LG's considerable emphasis on rendering shadowed subjects (see also Figure 16), detailing their features and contents with color *in the dark* is a strong theme in her small collection of work. Her "Aurelia/Lola" uses luminance contrast to great effect. Also, in "Forest Study" chromatic contrast is employed to produce halation effects — something anecdotally suggested by potential tetrachromat artists as a routine kind of perceptual experience arising from numerous color combinations.

Consider also the paintings of LA in Figure 14, which convey the chromatic palette she tends to employ as extremely varied and diverse. LA uses color very effectively as a structural feature — defining lines using chromatic and luminance contrast. She layers color to create veiling and translucence (e.g., "Mother O Mine") producing dimensions of emotion behind the canvas. Unlike works that use close to every pigment in the paintbox, LA's excess of color in no way feels gratuitous, but instead seems to invite one to look longer, analyze, untangle. Similarly, the shadowed regions of the paintings, while also complex, seem more intricate, buried and hiding important detail (e.g., "Guardian").

While the foregoing analyses are subjective and unsystematic, clearly some features of the LA and LG paintings are shared with those of CA. Whether these are features that are simply technique-based stylistic variations, or indicative of features present in a tetrachromat art genre, is an issue in need of systematic study.

7. Summary

In the present study we set out compare potential tetrachromat color perception with the perception of normal trichromat controls. Using Minimum-Motion at isoluminance tasks we found that one potential tetrachromat showed significant variation compared to normal trichromat control subjects, that is consistent with the processing of signals from a putative extra photopigment class. We discussed how other factors might be contributing to potential tetrachromat color perception variation, including the idea that color perception might be trained up and enriched by early developmental experience.

Section 3's psychophysical investigations provide a novel approach to assessing the effects of potential tetrachromat genotypes on perception. The preliminary data presented suggest that while some processing differences associated with tetrachromat genotypes may be very significant they are not global, and they do not always involve a heightening of perceptual processing. To our knowledge such subtleties have not been systematically described in previous empirical reports investigating the psychophysical functions underlying potential human tetrachromacy phenomena.

Section 4 evaluated preliminary explanatory models of the psychophysical results and found the empirically observed variation linked to the potential tetrachromat genotype seemed to be a result of both possession of an extra photopigment opsin gene and artistic training across the lifespan.

Section 5 proposed new procedures for simulating naturalistic scene processing under constraints imposed by one form of empirically-based tetrachromat filter. The simulations are informative and may prove valuable in more systematic investigations involving a larger study of potential tetrachromat perceptual processing.

We believe that analyses of the kind presented here, while preliminary, can lend insights into how potential tetrachromacy differs from normal trichromatic processing, and how observers with potential tetrachromacy may experience the world in ways that differ from individuals with trichromacy. It should be emphasized that the present proposal for designing tetrachromat filters does not yield an image conversion procedure that permits a trichromat observer to actually experience what a tetrachromat perceives. Image simulations that capture additional tetrachromat processing components — some of which may not be easily accommodated by trichromat cortical processing constraints — are likely to be difficult to communicate to trichromat observers. For this reason the proposed tetrachromat simulations provide only a means of referencing features of experience and natural scene processing, shown to be processed differently from those of trichromats under the empirical circumstances in which they were measured. The present investigations are our first attempt to develop and deliver such filters.

At present, science does not clearly indicate what to expect for tetrachromat perceptual processing, and it is uncertain whether potential tetrachromacy has an non-negligible impact on daily visual experience. It is unclear whether consequences of tetra chromat genotypes will be appear in tetrachromat artwork as greater uses of color, or if it will appear as more subtle uses of saturation, or through the representation of gloss or luster, or even whether it will be a difference that applies across global color space, or if it will be constrained to particular regions of color space and specific levels of luminance contrast. For these reason we think that attempting to develop filters based on empirical psychophysical data is a worthwhile approach for evaluating how observers with potential tetrachromacy may perceive the world differently compared to trichromat observers.

Figure 12. Original Oil "Memento." © Tuck Contreras. www.tuck.communicatingbydesign.com. Reproduced with permission.

Figure 13. Original Oil "Forces of Nature" © Tuck Contreras. www.tuck.communicatingbydesign.com. Reproduced with permission.

Figure 14. Original artwork by Louisa Antico. Works shown, left to right, are "Antheia" (left), "Guardian" (middle), "Mother O Mine" (right) © and courtesy of Louisa Antico: www.louisaantico.com. Reproduced with permission.

Figure 15. Original artwork by Lisa Guo. Works shown, left to right, are "Forest Study" (left), "Battle" (right). Lisa Guo © and courtesy of Lisa Guo. $jazzedyart.tumblr.com$. Reproduced with permission.

Figure 16. Original artwork by Lisa Guo. Works shown, left to right, are "Aurelia/Lola" (left), "Barracks" (right) © Lisa Guo. $jazzedyart.tumblr.com$. Reproduced with permission.

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Keith Goldfarb received his MS in Mathematics from the University of California, Berkeley (1985). He was a co-founder of Rhythm and Hues Studios, a pioneering visual effects company. In 2016 he was a recipient of a Technical Achievement award from the Academy of Motion Picture Arts and Sciences, in part due to his work on color matching at Rhythm and Hues. He is now working at Blackthorn-Media, a studio developing content for virtual reality.