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Task-dependent contrast gain in anomalous trichromats

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ABSTRACT

Anomalous trichromacy is a form of color vision deficiency characterized by the presence of three cone types, but with shifted spectral sensitivities for L or M cones, causing a red-green color deficiency. However, long-term adaptation to this impoverished opponent input may allow for a more normal color experience at the suprathreshold level ("compensation"). Recent experimental evidence points to the presence of compensation in some tasks. The current study used threshold detection, suprathreshold contrast matching, and a reaction-time task to compare contrast coding in normal and anomalous observers along the cardinal cone-opponent axes. Compared to color normals, anomals required more L-M contrast, but not S contrast, to detect stimuli and to match an achromatic reference stimulus. Reaction times were measured for several contrast levels along the two cone-opponent axes. Anomals had higher overall reaction times, but their reaction-time versus contrast functions could be matched to those of controls simply by scaling contrast by the detection thresholds. Anomalous participants were impaired relative to controls for L-M stimuli in all three tasks. However, the contrast losses were three times greater for thresholds and reaction times than for suprathreshold matches. These data provide evidence for compensation in anomalous trichromats, but highlight the role that the experimental task plays in revealing it.

1. Introduction

Typical human color perception is based on the activities of three types of cone photoreceptors in the retina which are maximally sensitive to short (S), medium (M) or long (L) wavelengths. Most current models of color vision hold that in the retina and lateral geniculate nucleus these cone signals are compared within two channels subserving color vision: one differences the activities of the L and the M cones (L − M) and the other compares the outputs of the S cones to the sum of the activity of the L and M cones (S − [L + M]) (Derrington, Krauskopf, & Lennie, 1984).

The spectral sensitivities of the cones are determined by which opsin protein is present in their photopigment, which is in turn determined by the sequence of nucleotides in the genes coding for these opsins (Nathans, Thomas, & Hogness, 1986). In normal trichromats, the peak sensitivities of the L and M cones differ by roughly 30 nm. However, the genes that code for the L and M opsins are located in a tandem array on the X chromosome, and have nearly identical nucleotide sequences (Nathans et al., 1986). This makes these genes especially susceptible to unequal homologous recombination (Neitz & Neitz, 2011), and these recombination errors are responsible for common forms of red-green color vision deficiency (CVD), which affect around 8% of Caucasian males (Nathans et al., 1986). Dichromacy generally occurs when there is only a single functional copy of the L or M pigment gene. Because there is no L-M signal, dichromats lack this dimension of color vision. In less severe forms of CVD, collectively called anomalous trichromacy, three different photopigment genes are expressed in the retina. However, the peak sensitivities of the X-linked photopigments are unusually close together (Neitz & Neitz, 2011), with either the L pigment shifted close to the M pigment (protanomaly) or the M pigment shifted close to the L pigment (deuteranomaly). The decreased spectral separation diminishes the difference signal, causing a loss in sensitivity, and difficulty discriminating colors along the red-green dimension. Notably, however, the spectral separation of the photopigments by itself is an imperfect predictor of discrimination ability (Barbur et al., 2008; Bosten, 2019; Crognale, Teller, Motulsky, & Deeb, 1998; He & Shevell, 1995; Hurvich, 1972; MacLeod, 2002).

Even if the L-M signals are reduced, this does not necessarily predict correspondingly weaker responses within the L-M pathway. The visual system is highly adaptable, and this adaptation can in principle

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compensate for variations in sensitivity to maintain consistent visual experience across space and time. For instance, the central few degrees of the retina is screened by macular pigment (Snodderly, Auran, & Delori, 1984). This pigment absorbs mainly short wavelength light, altering the spectrum of light that reaches the cones in the central versus the peripheral visual field. Despite this, the stimulus that looks white differs far less between the central and near-peripheral retina than the response of the receptors would predict (Webster & Leonard, 2008). Similarly, over time oxidative stress to the lens causes it to become darker and more yellow (Michael & Bron, 2011). However, this does not result in a percept of the world becoming successively darker and yellower, and in fact the percept of white remains stable over the lifespan (Delahunt, Webster, Ma, & Werner, 2004; Werner & Schefrin, 1993; Wuerger, 2013).

Adaptive adjustments may also compensate for variations in the contrast or strength of color signals. S cones make up a small fraction of the total cones in the retina, and are sparsely distributed compared to the longer-wavelength cones (Curcio et al., 1991; DeMonasterio, Schein, & McCrane, 1981). Moreover, the differences in cone signals mediating color are necessarily smaller than the additive signals conveying luminance. Yet subjectively the world does not appear more impoverished in chromatic than luminance contrast (McDermott & Webster, 2012). There is evidence that between the retina and cortex, the gain of the S-(L + M) mechanism is increased substantially (Mullen, Dumoulin, & Hess, 2008; Rabin, Switkes, Crognale, Schneck, & Adams, 1994), and the L − M system has much higher sensitivity than L + M in terms of cone contrasts, counterbalancing the mismatch in available cone signals (Chaparro, Huang, Kronauer, & Eskew, 1993). These adjustments may follow naturally from adaptation processes that calibrate sensitivity and neural gain according to the range of stimulation in the environment (Stringham, Sabatinelli, & Stringham, 2013; Webster & Mollon, 1997; Webster, Juricevic, & McDermott, 2010) in order to make optimal use of the limited response range available to neurons (Twer & MacLeod, 2001).

Given a lifetime of adaptation, perhaps the visual systems of anomalous trichromats are similarly able to compensate for their diminished sensitivity, providing an experience of the world that appears less diminished in color than their cone sensitivities predict (MacLeod, 2002; Webster et al., 2010). Whether this would also lead to better threshold discrimination depends on whether the gain of the L-M signal is increased prior or subsequent to the limiting noise (MacLeod, 2002). Several studies have examined the perceptual world of anomalous trichromats, with mixed evidence for neural compensation.

Multidimensional scaling (MDS) is a technique that can be used to build an n-dimensional perceptual space, where the distance between points is determined by the reported similarity between the points. Müller, Cavonius, and Mollon (1991) measured reaction times during a discrimination task for two deuteranomals and one color vision normal (CVN) participants and used MDS to reconstruct a theoretical color space based on these results. They found that the deuteranomalous space is dominated by the S-(L + M) dimension, and the L-M dimension appeared to be severely reduced. A number of other studies also found MDS-derived dichromat or anomalous spaces to be dissimilar to those of normal trichromats, consistent with their weaker spectral sensitivities (Bosten, Robinson, Jordan, & Mollon, 2005; Jordan, Deeb, Bosten, & Mollon, 2010; Paramei, 1996; Paramei, Izmailov, & Sokolov, 1991). More recently, Boehm, MacLeod, and Bosten (2014) also used MDS with a perceptual dissimilarity task, and found that the perceptual spaces of the anomalous participants were similar to those of normal participants. Importantly, this result was not predicted by the anomals' discrimination thresholds, which were substantially impaired relative to normals. This study provided strong evidence in support of compensation in anomalous trichromats. Similarly, Knoblauch, Marsh-Armstrong, and Werner (2020) used maximum likelihood difference scaling to measure the appearances of suprathreshold stimuli along the L-M and luminance axes. Anomalous trichromats' difference scales of the L-M stimuli, but not luminance stimuli, demonstrated an increase in contrast gain relative to controls, which points to a role for compensation in judgments of suprathreshold contrast.

In a different measure of suprathreshold color differences, Regan and Mollon used a perceptual grouping task varying amounts of L-M or S-(L + M) contrast to produce rival perceptual organizations, with the "winner" presumably depending on the salience of the respective dimension (Regan & Mollon, 1997). The results showed that for most anomalous trichromats, the salience of the L-M stimuli was again reduced relative to color normals. Intriguingly, though, two of the anomals had a perceptual balance more similar to the control participants.

Chromatic sensitivity in CVDs has also been examined using visual evoked potentials (VEPs) to stimuli designed to selectively change the activity of single cone types (e.g. Rabin et al., 1994). When anomalous trichromats are shown these stimuli monocularly, their VEPs demonstrate reductions in the amplitude and latency of signals corresponding to their deficient cone type (Crognale et al., 1993; Rabin, Kryder, & Lam, 2016, 2017). Yet Rabin, Kryder, and Lam (2017) recently reported that when CVD participants instead view their cone-isolating stimuli binocularly, their VEPs have significantly greater amplitude than when viewed monocularly, and closer to color normals. In another neurophysiological experiment, Tregillus et al. (2020) used fMRI to compare cortical responses to L-M stimuli in anomalous trichromats and color-normal participants. They found a significant difference in the chromatic contrast response functions of the two groups in primary visual cortex (V1), but no difference in later regions of early visual cortex (V2 and V3).

Thus the degree to which the visual systems of anomalous trichromats are compensating for their impoverished L-M signal remains uncertain, and may depend on the task chosen to probe the responses and on the consequent nature or basis for the compensation. In particular, many of the studies reporting enhanced chromatic responses tend to rely on subjective reports, and leave open the possibility that these responses could reflect criterion effects rather than actual sensitivity gains. The aim of the current study was to explore the effect of the task on compensation by comparing the chromatic responses derived from two very different measures of suprathreshold contrast responses: one based on suprathreshold contrast matching (SCM) and the other on reaction times for discriminating suprathreshold differences. SCM is a well-established and reliable method for equating perceptual salience along different chromatic or luminance axes (e.g. Switkes, 2008; Switkes & Crognale, 1999; Tiippana, Rovamo, Näsänen, Whitaker, & Mäkelä, 2000; Vanston & Crognale, 2018), and was used to provide a "subjective" measure of how strong the L-M and S dimensions appear to anomals. Reaction times, which show a linear monotonic decrease with increasing stimulus contrast (McKeefry, Parry, & Murray, 2003; Plainis & Murray, 2000), were alternatively used to provide an objective "performance measure" of the chromatic contrast responses. In addition to any difference between the two tasks attributable to criterion effects, reaction times and contrast matching may be governed by different neural substrates which could in turn be differentially susceptible to compensation. Both measurements were compared to observers' detection thresholds to assess whether either task might reveal suprathreshold compensation.

2. Methods – Experiment 1

2.1. Participants

Seven anomalous trichromats (six male, mean age 24), and seven color-normal control participants (four female, mean age 28) participated in Experiment 1. Participants were initially screened for color vision deficiency using standard pseudoisochromatic plate tests (38-plate Ishihara test, HRR test, Dvorine Color Plates, Cambridge Color Test). Both color normal and color vision deficient (CVD) participants

then completed Rayleigh matches on an HMC anomaloscope, and diagnosis was based on standard match ranges and midpoints. Rayleigh match ranges and CCT thresholds are shown in Table 1.

Participants who were classified as dichromatic were excluded from the current study. Participants had normal or corrected-to-normal visual acuity and gave informed consent to participate. Prescription corrective lenses, when used by subjects, were non-tinted. Procedures were first approved by The University of Nevada, Reno's human subjects institutional review board and were in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2. Apparatus

Stimuli were presented on a Sony Trinitron MultiScan E540 CRT monitor with a refresh rate of 85 Hz in a darkened room. Stimuli were generated and presented using a ViSaGe MkII graphics card (Cambridge Research Systems) with 14-bit color resolution, specified with linearized lookup tables, and calibrated using a PR-655 SpectraScan spectroradiometer (Photo Research).

2.3. Stimuli – Experiment 1

Stimuli were horizontally oriented circular Gabor patches with a spatial frequency of one cycle per degree and subtending 10 degrees of visual angle. The Gaussian envelope had a standard deviation of two degrees and a full width at half maximum of 4.7 degrees. Patch chromaticities were defined by modulations along the L-M or S-(L + M) axes around a common mean gray point in a cone-opponent space approximately scaled by nominal multiples of threshold for color-normal observers (Webster, Miyahara, Malkoc, & Raker, 2000).

The chromaticity coordinates of the axis endpoints are given in Table 2. All stimuli were presented on a neutral gray background with the same space-averaged chromaticity and luminance to keep constant the adaptive state of the participants. The mean chromaticity of the display was set to the chromaticity of CIE Illuminant C (x = 0.31, y = 0.32) and the mean luminance was 18 cd/m^2. A minimum motion task was used to determine the isoluminant plane for each individual participant (Anstis, Cavanagh, Mollon, & Sharpe, 1983).

2.4. Procedure – Experiment 1

Participants were seated 114 cm from the monitor and maintained fixation on a small point in the center of the screen (subtending 0.1 degrees of visual angle). Both detection thresholds and suprathreshold contrast matches were measured using a temporal 2AFC task, with stimuli presented with a square-wave onset/offset. In the detection threshold task, each temporal interval had a one second duration, and was accompanied by a beep. Participants indicated with a key press which of the two intervals contained a stimulus. Performance was tracked using two randomly interleaved staircases, with contrast adjusted using a two-down, one-up rule, yielding an estimate of the 70.7% threshold. For each staircase, after the first two reversals were recorded, the contrast step size was changed from 0.2 to 0.05 log units, where it remained for the duration of the staircase. Testing terminated when both staircases reached ten reversals; the last eight reversals were averaged to yield the participant's detection threshold. The L-M and S axes were tested in separate back-to-back runs, each typically taking ~5 min, and the order of axis presentations was counterbalanced across participants. Detection thresholds for luminance-modulating stimuli were also measured for a subset of participants (six controls and five anomals) in a separate session.

In the suprathreshold contrast matching task, one temporal interval contained a reference stimulus, and the other contained a test stimulus. The reference stimulus was an achromatic Gabor patch with a fixed Michelson contrast of 2.8% (~4.7 times the mean control detection threshold), and participants responded with a key press whether the chromatic grating appeared to have a stronger or weaker contrast. The test stimulus varied in contrast using the same staircase procedure as the threshold task, and alternated between the L-M and S axes on consecutive trials. Each temporal interval had a duration of one second and was accompanied by a beep, and the two intervals were separated by a blank screen (with fixation point) shown for one second. The presentation order of test and reference stimuli was randomized.

Experimental outcomes were compared to each other using null hypothesis significance testing. When multiple comparisons are made, the possibility of Type 1 errors is controlled for using the false discovery rate (FDR) method described by Benjamini and Hochberg (1995), with the proportion of allowable Type 1 errors (q) set to 0.05. All p values reported have been FDR-corrected when multiple comparisons were made.

Table 1
Anomalous participant diagnoses and test results. Match Range is each participant's Rayleigh match range expressed as a proportion of the total range of mixtures available (e.g. a score of 0.25 indicates that participants matched R & G light mixtures across 25% of the total possible range). P, D, and T are the discrimination thresholds along the protan, deutan, and tritan confusion lines measured using the CCT test. Mean saturation has been multiplied by 10^3, the default on the device used, but this scaling is arbitrary.

Participant	Diagnosis	Match Range	P	D	T
A01	Protan	0.06	101.61	21.09	4.88
A02	Protan	0.25	14.7	37.36	8.85
A03	Protan	0.08	110	19.11	7.74
A04	Protan	0.08	97.36	23.66	13.82
A05	Deutan	0.1	29.87	54.8	15.35
A06	Deutan	0.04	8.12	14.1	17.68
A07	Deutan	0.1	28.88	20.5	18.36

Table 2
CIE 2006 2 deg chromaticity coordinates of the endpoints for each chromatic axis.

Axis endpoint	x	y
L − M	0.387	0.280
M − L	0.219	0.365
S − (L + M)	0.300	0.269
(L + M) − S	0.323	0.382

3. Results – Experiment 1

Detection thresholds and suprathreshold matches were measured for each participant. Since the measure of interest in this experiment is the relationship between anomalous and control performance, the data are expressed as ratios of cone contrasts, which we designate ρ. For L-M detection thresholds, for instance, each anomalous participant's threshold L-M cone contrast was computed as:

$$\sqrt{L_C{}^2 + M_C{}^2}$$

where L_C and M_C are the Michelson cone contrasts for the L and M cones, and this threshold was divided by the mean control L-M threshold to yield a ρ value for that subject. S cone contrasts are simply the Michelson cone contrasts for the S cones. Given that the anomalous participants' L and M cone peak spectral separations were unknown, cone contrasts for both controls and anomals were calculated using the Stockman & Sharpe 2-deg fundamentals (Stockman & Sharpe, 2000). Detection thresholds for L-M and S stimuli are shown in Fig. 1; anomalous thresholds are plotted as multiples of the mean control threshold in Fig. 2. On average, anomals' L-M thresholds were 6.36 times higher than controls', thus the detection threshold L-M $\rho = 6.36$. The corresponding S axis value for this task was $\rho = 1.58$. LUM detection thresholds are shown in Fig. 3—anomals' LUM thresholds were lower than those of controls, with LUM $\rho = 0.68$. These results are further discussed in Section 6.

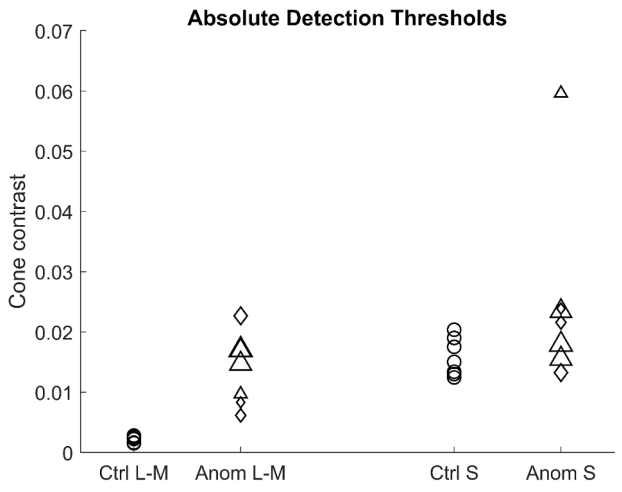

Fig. 1. Detection thresholds for L-M and S modulating stimuli. Data were collected using a temporal 2AFC task, and are shown here for seven control and seven anomalous participants. See text for definition of cone contrast. One anomalous subject with S threshold of ~0.06 can be considered an outlier at 2.2 standard deviations above the mean; this data point was nonetheless included in analysis. Circles = controls, triangles = protanomals, diamonds = deuteranomals. For anomals, symbol sizes are scaled by each participant's CCT threshold. Correlation between anomalous L-M detection thresholds and CCT thresholds (for deficient axis) was r = 0.65 (p = 0.12).

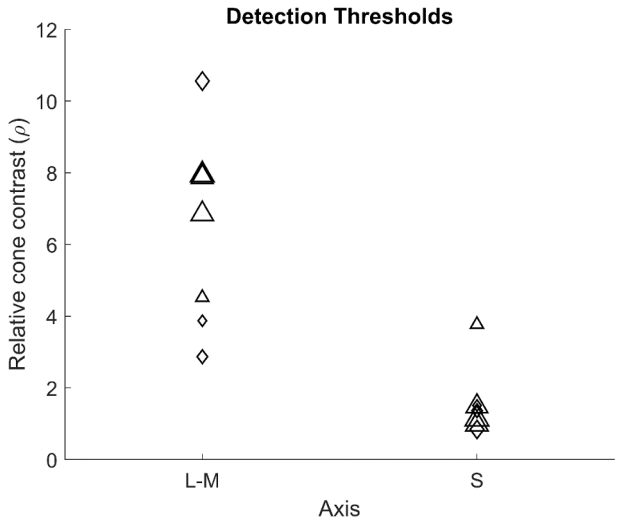

Fig. 2. Detection thresholds of anomalous trichromats for L-M and S modulating stimuli, expressed as multiples of the mean control thresholds. Data were collected using a temporal 2AFC task, and are shown here for seven anomalous participants. The mean control threshold was based on data from seven control participants. See text for definition of cone contrast. Triangles = protanomals, diamonds = deuteranomals. Symbol sizes are scaled by each participant's CCT threshold.

Suprathreshold contrast matching results are shown in Fig. 4. The ρ values for the contrast matching task were 2.1 and 1.19 for the L-M and S axes respectively.

4. Methods – Experiment 2

In the second set of experiments we turned to a different measure of the contrast response based on reaction times. Any differences observed between contrast matching and reaction times for suprathreshold stimuli could be due to the processing stages or pathways underlying participant performance. These could differ between the two tasks, and may be unequally affected by compensation.

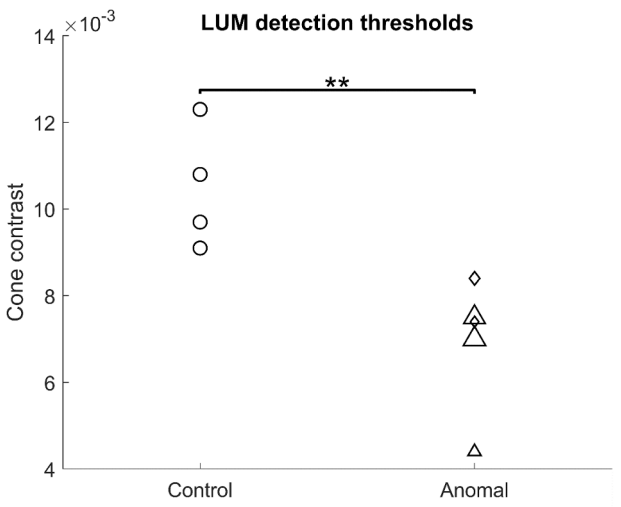

Fig. 3. Detection thresholds for LUM modulating stimuli. Data were collected using a temporal 2AFC task, and are shown here averaged across six control and five anomalous participants. Asterisks indicate statistical significance: 2 asterisks denote $p < 0.01$. Circles = controls, triangles = protanomals, diamonds = deuteranomals. For anomals, symbol sizes are scaled by each participant's CCT threshold.

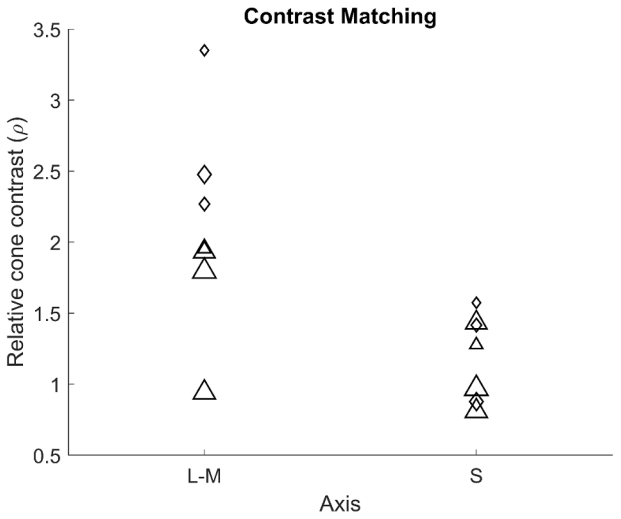

Fig. 4. Suprathreshold contrast matches for L-M and S modulating stimuli. Chromatic stimuli were matched to a fixed-contrast achromatic reference stimulus. Data were collected using a temporal 2AFC task, and are shown here for seven control and seven anomalous participants. See text for definition of cone contrast. Note that the y axis has changed from Fig. 2. Triangles = protanomals, diamonds = deuteranomals. Symbol sizes are scaled by each participant's CCT threshold.

4.1. Subjects

The same seven anomalous trichromats and seven controls from Experiment 1 also participated in Experiment 2.

4.2. Stimuli – Experiment 2

Stimuli were solid colored squares subtending 10 degrees of visual angle, which could be presented within either of two square black outlines located on the left and right sides of the screen and centered at 7.5 degrees eccentricity from a central fixation point. These stimuli were

chosen for Experiment 2 for several reasons. The black outlines created well-defined spatial locations where the stimuli would appear, and prevented participants from using any residual luminance contrast between the stimulus and background as a cue to the stimulus (see Procedure, below).

Colors were sampled from unipolar excursions along each of the four cone-opponent directions: L − M, M − L, S − (L + M), and (L + M) − S, referred to here as L+, L-, S+, and S−, respectively. For the main experiment, colors along each axis were sampled at four contrast levels; six control participants were also tested at four lower contrasts. All stimulus contrasts for Experiment 2 are shown in Table 3.

Reaction times for luminance-modulating stimuli were measured for a subset of participants (six controls, three anomals). On each trial, achromatic LUM stimuli were randomly chosen to be either increments or decrements relative to the background. There were four luminance levels sampled: 1, 2, 4, and 8 cd/m^2 above or below the background luminance (corresponding to Weber contrasts of 5.6%, 11.1%, 22.2%, & 44.4%).

4.3. Procedure – Experiment 2

Subjects were seated in a dark room 114 cm from the screen. On each trial, the test stimulus was presented either on the left or the right, with a temporal cosine envelope that peaked in contrast at 260 ms. While maintaining fixation, participants reported with a button press which side of the screen the stimulus was presented in. Subjects were instructed to respond as quickly as possible while still maintaining high accuracy. Reaction time was measured using the GetSecs function from the Psychophysics Toolbox (Brainard, 1997) for MATLAB (MathWorks). This function was used to query the current time at the beginning of stimulus onset and when the subject's button press was detected by the software; the difference between these two points was defined as a reaction time. We have no independent measurement of the time at which the subject pressed down the key, so the temporal resolution of our reaction time data is limited. Nonetheless, the comparisons of interest are between control and anomalous subjects, and the noise in our measurements can safely be assumed to be similar between the two groups.

Each contrast level along each of the four axes was presented 30 times; only trials where the participant answered correctly were included in the final analysis. In addition, participant accuracy was tracked, and conditions wherein the participant responded correctly on fewer than 80% of trials were excluded from further data analysis. Sample reaction time distributions are shown in Fig. 5. Many such distributions for both controls and anomals were found to be positively skewed, a feature common to reaction time data. Because of this, medians were used as measures of central tendency when considering individual participant data (as in the function fitting described below). Analyses based on group means used the mean across medians.

A linear function was fit to each participant's reaction time data; this was done independently along each of the four axes. The function used was a modified Piéron equation, which has been shown to provide a good fit for reaction time data as a function of stimulus contrast (McKeefry et al., 2003; Plainis & Murray, 2000). This function takes the form:

$$RT = RT_0 + k \cdot 1/C$$

where RT is the reaction time, RT_0 is the asymptotic RT, k is the slope, and C is the cone contrast, defined as in Experiment 1.

4.4. Results – Experiment 2

Reaction times averaged across participants are plotted against inverse cone contrast in Fig. 6. Anomals had longer reaction times than controls at all contrasts along the L-M and S axes. Their contrast-reaction time function slopes were steeper, with their reaction times near those of controls at the highest contrasts. Between-participants variances in reaction times were higher for lower contrasts in anomals. This is partially because not all anomalous participants could reliably detect all stimulus contrasts, and thus the mean reaction times at lower contrasts tended to be based on fewer data points. Table 4 shows the number of participants included in the mean at each contrast level.

To characterize the differences in reaction times, we assumed that the anomalous responses were the same as the normal responses at a lower contrast, and thus determined the degree to which the anomalous contrasts would need to be scaled in order to fit the control data. To do this we multiplied each anomalous contrast level by a scalar, which was varied to minimize the mean squared error between each scaled anomalous reaction time and its corresponding point on the control function. For this analysis it was necessary to collect additional data for the control observers at lower contrasts, to compare with the "effectively low" contrast for the anomalous observers. This analysis was done individually for each participant for the L-M and S axes. The resulting scaled RT functions are shown in Fig. 7. The mean L-M scalar across participants was 10.9, and the mean S scalar was 2. Since these scalars represent the ratio of anomalous to control contrast loss, they were used as the ρ values for the reaction time task. The luminance reaction time functions did not differ between the groups.

5. Comparing task performance

The ρ values for the three tasks are shown in Fig. 8. To evaluate relative anomalous performance, we compared the ρ values using paired-samples t tests. The L-M ρ values were significantly lower for the contrast matching task than for the detection task [$t(6) = 3.75$, $p < 0.05$, $d = 2.13$], while the detection and reaction time tasks did not differ significantly [$t(6) = 1.02$, $p = 0.35$]. Similar comparisons for the S axis revealed no significant difference between detection thresholds and contrast matching [$t(6) = 1.10$, $p = 0.47$] or detection thresholds and reaction times [$t(6) = 0.30$, $p = 0.77$].

Anomals showed impairment in reaction times to L-M stimuli with a magnitude similar to that observed in their detection thresholds, while their suprathreshold L-M contrast matches were more similar to those of controls. This pattern did not hold for their responses to S axis stimuli, which did not differ significantly across the three tasks.

6. Discussion

In order to investigate whether anomalous trichromats show evidence of perceptual compensation along their deficient L vs, M dimension, we measured detection thresholds (DT), suprathreshold contrast matches (SCM), and reaction times (RT) for seven controls and seven anomals. As expected, anomals needed more L-M cone contrast to detect centrally presented Gabor stimuli compared to controls. They also required more L-M contrast than controls to match an L-M stimulus to a

Table 3
All stimulus cone contrasts used in Experiment 2, calculated as described in Section 3.

Axis	Experiment 2 stimulus cone contrasts							
L − M	0.0015	0.0030	0.0046	0.0061	0.0076	0.0153	0.0309	0.0630
M − L	0.0015	0.0030	0.0045	0.0060	0.0075	0.0150	0.0298	0.0586
S − (L + M)	0.0087	0.0173	0.0258	0.0341	0.0422	0.0811	0.1500	0.2609
(L + M) − S	0.0089	0.0180	0.0272	0.0366	0.0461	0.0968	0.2143	0.5454

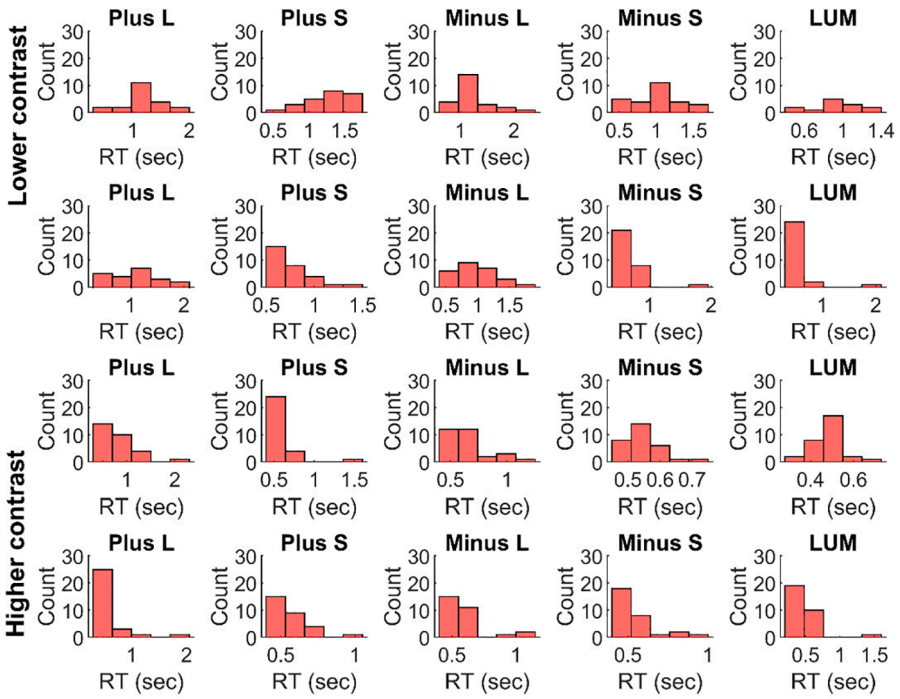

Fig. 5. Reaction time distributions of the four highest contrasts for subject A03. Many such distributions are positively skewed, as is common for reaction time data. Note that that abscissae vary across plots for aesthetic purposes.

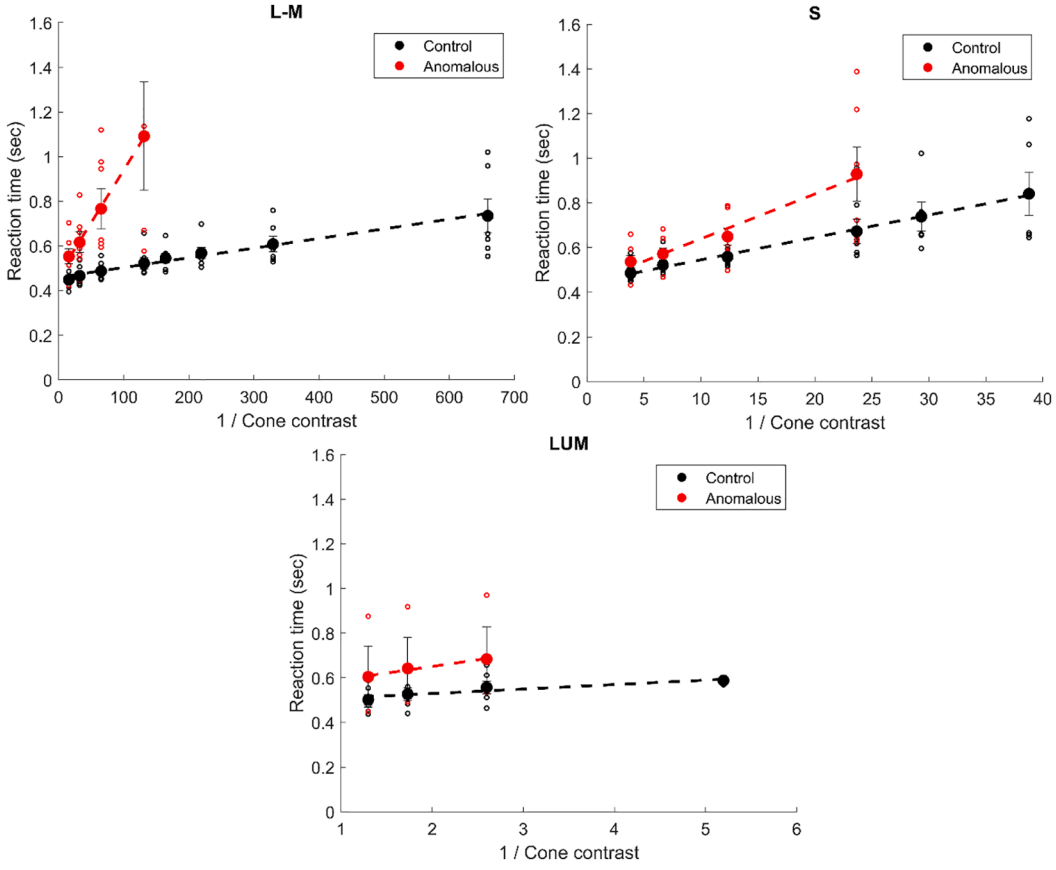

Fig. 6. Reaction times as a function of inverse cone contrast. Note that on this abscissa, lower contrasts are rightward and higher contrasts are leftward. Black dots are reaction times averaged across control subjects, and red dots are reaction times averaged across anomalous subjects. Open symbols are individual sample medians. Black and red dotted lines represent the best fitting linear functions for controls and anomals, respectively (see text). Error bars represent ±1 standard error of the mean. See Table 4 for numbers of subjects in each condition.

Table 4
Number of participants included in the mean data for each contrast level. Participants were excluded from a given condition if they failed to reach a criterion percent of correct responses for that condition (see text).

Condition	Lowest contrast							Highest contrast
L-M control	6	6	6	6	7	7	7	7
L-M anomal	0	0	0	0	4	7	7	7
S control	0	2	5	5	7	7	7	7
S anomal	0	0	0	0	6	7	7	7

comparison achromatic stimulus. However, anomals' performance on the SCM task was three times closer to normals' than it was on the DT task, which is the result predicted by partial neural compensation. In contrast, anomals' reaction times for detecting chromatic stimuli were not significantly different from that predicted by their detection performance.

The observed difference in ρ values represents the magnitude of the compensation effect seen in SCM. The discrepancy we find between threshold and suprathreshold results are similar to those of Boehm et al. (2014), who found that the perceptual spaces of anomalous trichromats, measured using multidimensional scaling, were closer to that of normals than predicted by the difference between the two groups' performance on a discrimination task. A similar result was also obtained by Emery, Parthasarathy, Joyce, and Webster (2021), who used a hue scaling task to show that the salience of red and green in a suprathreshold stimulus were greater for anomals than predicted by their thresholds. However, when the contrast response was instead assessed with reaction times in the current study, anomals showed a level of deficiency predicted by the threshold detection task. Thus in this case there was little evidence for suprathreshold compensation.

This could be because reaction times and apparent contrast depend on different pathways or processes. For example suprathreshold apparent contrast is largely independent of spatial frequency even though threshold sensitivity is much higher for medium frequencies, and this is likely to reflect cortical gains (Georgeson & Sullivan, 1975). Yet reaction times are strongly dependent on spatial frequency, and this dependence has been used to argue that reaction times are limited by precortical stages of processing (Plainis & Murray, 2000). A similar difference may underlie the differences we observed in the two tasks for chromatic contrast. However, at least some aspects of reaction times for contrast may have cortical basis. Webster and Mollon (1994) showed that reaction times are affected by contrast adaptation, which is itself thought to reflect sensitivity changes in the cortex. To the authors' knowledge, the only other study to compare the reaction times of color normals and anomalous trichromats along the cone-opponent axes is that of Müller et al. (1991). The reaction times in that study were measured in service of multidimensional scaling, and the raw reaction time data are not shown. However, they also concluded that the deuteranomals showed no evidence for perceptual compensation.

Without neuroimaging or electrophysiology, any conclusions to be drawn about the neural sites underlying our results are necessarily speculative. While previous work supports the adaptability of precortical color signals (Chang, Hess, & Mullen, 2016; Gollisch & Meister, 2010; Solomon, Peirce, Dhruv, & Lennie, 2004), contrast adaptation seems to be stronger in visual cortex (Kohn, 2007), especially within the pathway carrying the L-M opponent signal (Lutze, Pokorny, & Smith, 2006). Rabin et al. (2017) found EEG evidence for compensation in anomalous trichromats, but only when stimuli were viewed binocularly,

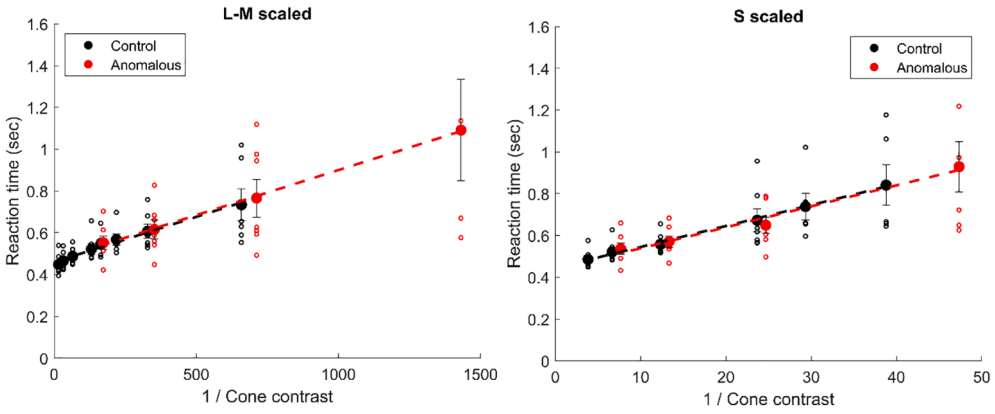

Fig. 7. Reaction times shown as in Fig. 6. Black points are data averaged over control subjects, and red points are data averaged over anomalous subjects. Open symbols are individual sample medians. Contrasts for anomalous subjects have been scaled to best fit the control data. These scalars were 10.9 for the L-M axis and 2 for the S axis. Dotted lines are the best fits by a linear function (see text). Error bars represent ±1 standard error of the mean. See Table 4 for numbers of subjects in each condition.

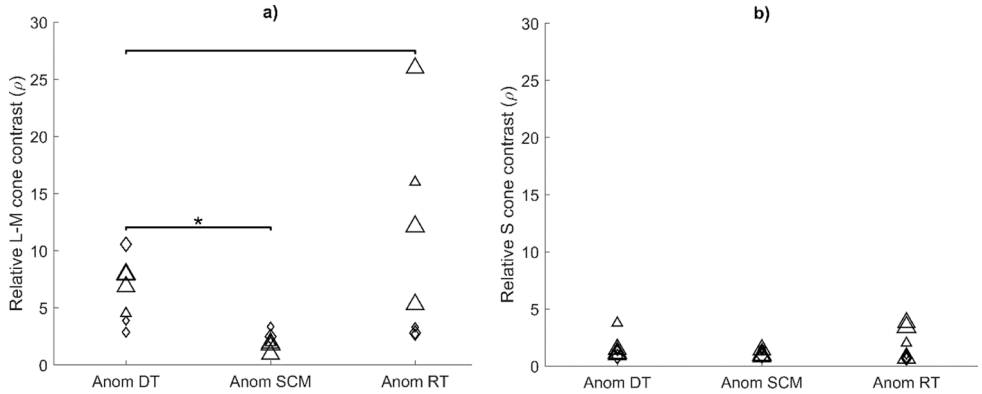

Fig. 8. a) Measured L-M ρ values for each of the three tasks. From left to right: anomalous L-M threshold ρ, anomalous contrast match ρ, anomalous reaction time ρ. Asterisks indicate statistical significance: 0 and 1 asterisks denote $p > 0.05$ and $p < 0.05$, respectively. b) Measured S ρ values for each of the three tasks. The three distributions were not significantly different. Triangles = protanomals, diamonds = deuteranomals. Symbol sizes are scaled by each participant's CCT threshold.

indicating that compensation is occurring cortically but prior to the combination of signals from the two eyes. Recent fMRI work supports the notion that compensatory mechanisms might exist in the early visual cortex of anomalous trichromats, with signs of compensation occurring in V2 and V3, but not in V1 (Tregillus et al., 2020). Perhaps detection thresholds in the current study were governed by V1 neurons, while the suprathreshold contrast matching task employed more anterior neural populations. By the same logic, we can say that it is unlikely that the reaction times were determined by highly adaptable cortical sites.

The stimuli in Experiment 1 were one cycle per degree Gabors presented foveally, while the stimuli in Experiment 2 were uniform squares presented at 7.5 deg eccentricity. Given that many visual functions vary with eccentricity and spatial frequency, could the difference in compensation strength between the two experiments be due to these factors? To our knowledge, the impact of eccentricity, spatial frequency, and other spatiotemporal attributes on adaptive compensation have not been systematically studied. However, evidence for such compensation has been demonstrated using varied stimuli: Gabors (Knoblauch et al., 2020), checkerboards (Rabin et al., 2017), uniform discs (Boehm et al., 2014), and radial gratings (Tregillus et al., 2020). Apart from contrast, low-level stimulus properties appear not to be critical in determining the degree of compensation demonstrated by anomals.

As noted in Section 3, cone contrasts were computed for anomalous subjects using the same spectral sensitivities as controls. For a given pair of chromaticities along the L-M axis (e.g. one reddish and one greenish), decreasing the spectral separation between the L and M sensitivities decreases the L-M cone contrast between those points. One alternative to the approach used here is to assume some shorter spectral separation and estimate anomalous cone contrasts accordingly. The effect of such an approach would be that anomalous detection thresholds and contrast matches would have lower L-M cone contrasts and would more closely resemble the control results.

All stimuli presented to subjects, as well as the background, had a space-averaged luminance of 18 cd/m^2, which is within the response range of rod photoreceptors. Since rod activity has been found to influence color perception (Stabell & Stabell, 1994; Stromeyer, 1974) in a manner that scales linearly with rod contrast (Cao, Pokorny, Smith, & Zele, 2008), we calculated the rod contrasts produced by a subset of the stimuli used. The maximum contrasts along each of the cardinal directions are listed in Table 5. Rod contrasts for chromatic stimuli ranged from 3% in the (L + M)-S direction to 15% in the L-M direction. Rod contrast was highest for the L + M direction, with a maximum of 44%. Rods are therefore unlikely to have contributed significantly to the appearance of the chromatic stimuli, especially considering that most stimulus contrasts in the current study were below this maximum.

Rods are more sensitive than cones. Since the most sensitive mechanism should dictate a detection threshold, could the anomalous subjects' chromatic thresholds be due to rod activity? The most common model of anomalous trichromacy, which we use here, assumes that the spectral sensitivities of the photoreceptors are identical to those of a normal trichromat except for the shifted sensitivity of the affected cone type. If this is the case, then control and anomalous subjects should have similar rod thresholds. Given the observed difference between the groups in L-M thresholds, these measurements were unlikely to have been governed by rod activity. The S axis detection thresholds were similar for controls and anomals; we cannot definitively rule out rod intrusion in this condition. Rod activity is unlikely to have played a major role in reaction time measurements, given their lower response latency relative to cones.

An unexpected finding was the difference in LUM thresholds between anomals and controls, particularly because anomalous participants' thresholds were lower than controls' (these data are shown in Fig. 3). Unsurprisingly, most studies on anomalous trichromats have focused on their color vision. While it has been theorized that reduced chromatic input to the parvocellular pathway might cause an increase in achromatic sensitivity, most studies directly comparing CVD and CVN participants on this dimension found no such difference (Knoblauch et al., 2020; Lutze et al., 2006; Wenzel, Ladunga, & Samu, 2001). Given the mesopic conditions of this experiment, it is possible that the LUM stimuli were being detected by rods. However, anomals have been shown to have scotopic sensitivity similar to controls (Simunovic, Regan, & Mollon, 2001). One recent study reported higher sensitivity to achromatic contrast in anomals (Doron et al., 2019), although this effect was seen only with spatial frequencies of six and nine cycles per degree. Contrast sensitivity at three cycles per degree was higher for anomals than controls, although not significantly so, and this spatial frequency is higher still than the one cycle per degree used in the current study. While LUM thresholds were only measured for six controls and five anomals, the effect was robust ($p < 0.005$, $d = 2.43$). On the other hand, as noted above the anomalous and normal observers did not differ in their reaction times for suprathreshold luminance contrasts. We do not know the basis for this difference.

Table 5
Rod contrasts for the endpoints (maximum contrast) of the four chromatic axes and one luminance axis.

Axis	Rod contrast
L − M	0.15
M − L	0.11
S − (L + M)	0.04
(L + M) − S	0.03
L + M	0.44

7. Conclusions

We have shown that while the detection thresholds of anomalous trichromats along the L-M dimension are elevated relative to those of color normals, contrast matching at the suprathreshold level is more similar between the two groups, suggesting a role for postreceptoral gain. However, these gains were not found when effective contrast was assessed with reaction times, which were instead consistent with their threshold losses. These results suggest that the degree of compensation observed for a color deficiency depends on the task used to probe the responses and on the sites and factors limiting different tasks.

CRediT authorship contribution statement

John E. Vanston: Methodology, Software, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization. **Katherine E.M. Tregillus:** Methodology, Software, Formal analysis, Investigation, Writing - review & editing. **Michael A. Webster:** Conceptualization, Methodology, Formal analysis, Resources, Writing - review & editing, Supervision, Funding acquisition. **Michael A. Crognale:** Conceptualization, Methodology, Formal analysis, Resources, Writing - review & editing, Supervision, Funding acquisition.

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