

University of Nevada, Reno

Perception of Warm and Cool Colors

A dissertation submitted in partial fulfillment of the requirements for the degree of
Doctor of Philosophy in Neuroscience

by

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ABSTRACT

Warm and cool judgements of color perception are a fundamental aspect of visual experience. Very few studies have been conducted on this aspect of perception and only recently has this dimension of color perception gained traction in the visual sciences. In this work, I examine the nature of warm vs cool judgements, what dimension they inhabit in color processing, how we perceive them, and how warm-cool hues influence visual adaptation. In the first study, I examine how individuals categorize colors in cone-opponent space and how ratings of warm versus cool map onto asymmetries inherently found in perceptually uniform color spaces. In the second study, I explore the reason for this asymmetry and why the warm-cool dimension aligns well with it by using a visual search paradigm to test the salience characteristics of hues. In the third and final study, I test differences between the warm and the cool dimension using a threshold task to examine which side (warm or cool) dominates perception. Together, these studies should provide a picture of the nature of warm-cool judgements and what colors we are most adapted to given our visual diets.

Dedication

To Anthony Ding, Kim Brogan, and Tim Brogan-Ding who gave me a home and a family when I needed it most. From watching football finals to the lunches and dinners when I visited San Diego, I always look forward to seeing you all when I am in town. Your love and care kept me striving throughout my doctoral career. Tony and Kim who have been a father and mother to me (you gave me a glimpse into what having loving parents is like and I am constantly overwhelmed by your generosity) and to Tim who has been a brother, your kindness gave me the strength and courage to take risks. Tony, you inspired me to become a teacher and an academic (so, I blame you); you inspired me to pursue higher education when the only degree I had was a high school diploma. Now, I've even pursued the highest degree possible; you are my hero and I strive to follow your example in life (such as your kindness)... following your humour on the other hand... questionable. If I get even close to being someone like you, I would be content in life. Thanks for making me tea every morning. The love you all have shown me I cannot express my gratitude enough for. I can only hope that I have made you proud. I love you all dearly...

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Chapter 1. General Introduction

Color naming, color judgement, and color emotions seem like learned constructs that have little to do with biological processes that govern perception and adaptation. Labels associated with particular hues, e.g., like vs dislike, clean vs dirty, light vs heavy, or warm vs cool, seem like arbitrary concepts that we use mainly for the purpose of color communication (Gibson et al., 2017). However, there may be a case to implement these judgements onto our adaptive capacities which may be governed by cone-opponent mechanisms from the lateral geniculate onto the visual cortex. Color biased regions along ventral visual pathway have been shown to be not only object and food selective, but the hues associated with these objects represent warmer hues with higher color saturation (Pennock et al., 2023). Cone-opponent processes, i.e., red vs green and blue vs yellow, were also shown to have lower sensitivities towards blue-yellow channels than to red-green (Goddard et al., 2010; Mullen et al., 2015) and that these weaker sensitivities seem to match what was found concerning asymmetries in saturation strength within perceptually uniform color spaces (McDermott & Webster, 2012). Hence, the notion that certain color judgements do not have a biological basis does not seem to hold muster; at least, there does seem to be some credence to warm vs cool judgements and their perceptual and biological correlates.

Behaviorally, lower sensitivities to blue-yellow and warm-cool compared to red-green have been shown in visual search tasks (Manalansan et al., 2025; McDermott et al., 2010). These tasks demonstrate how we almost discount blue-yellow hues in foraging-like tasks especially when compared with scenes which depict a higher concentration of red-green hues. This lower sensitivity to blue-yellow might be due to how much we are adapted to these colors and how little red-green we are exposed to in the environment. Blue-yellow and warm-cool occupy similar cardinal directions in color spaces. With blue-yellow, this has been shown to be representative of

the chromatic distributions of natural scenes, or outdoor environments, possibly owing to the amount with which we are adapted to this color direction (Skelton et al., 2024a). However, it still is a mystery as to how warm-cool occupies a similar direction of color space as blue-yellow and how much the warm-cool dimension occupies the asymmetries inherent in uniform color spaces (Manalansan & Webster, 2023). The projects presented in this dissertation aim to assess the very nature of warm-cool judgements and how representative of a color dimension it is. The motivation and goals for each project/chapter are highlighted below.

The first project was one of the first to highlight the close association between warm-cool colors and their association to asymmetries (or the areas we are least sensitive to) found in perceptually uniform color spaces such as CIEL*a*b*. Influenced by the notion that warm colors are associated with objects and cool colors are associated with the environment (Conway et al., 2020), we investigated how the hues themselves are categorized by individuals and how the categorization of hues into warm-cool categories correspond the unique hues. Initially, I had found stable judgements of these hues despite individual differences in culture, sex, and age amongst my participants. Despite how individuals may differ cognitively, people seem to reliably rate colors similarly between each other. Upon closer analysis of the data, these judgements were found to align well with asymmetries in CIEL*a*b* space originally found previously by McDermott & Webster, 2012. What this suggests is that, much like blue-yellow, warm-cool is a color dimension we are least sensitive to. We had also found that the warm-cool dimension is its own unique color dimension separate from blue-yellow. These findings put into question what colors we are most adapted to and where the warm-cool direction actually comes from.

For my second project, I determined the relative salience of warm-cool and blue-yellow colors in a visual search paradigm similar to that of McDermott et al., 2010. I compared the salience of these two dimensions in a foraging like task and compared reaction times to the reaction times of targets shown along backgrounds with chromaticities aligned to the orthogonal

directions of warm-cool and blue-yellow. These orthogonal directions represent reddish-green axis of cone-opponent space. We had found faster reaction times for targets presented in front of warm-cool and blue-yellow backgrounds compared to their reddish-green counterparts. Targets in front of the orthogonal backgrounds were more slowly found. This seems to suggest that reddish-green distractors are more perceptually demanding, i.e., they take up more attention and we attend to them much more than warm-cool or blue-yellow. This could be that we are more adapted to warm-cool and blue-yellow and there are much less reddish-green hues in the environment. This again corroborates previous findings in neuroimaging that brain regions have higher responses to red-green than to blue yellow (Goddard et al., 2010, 2019; Mullen et al., 2015).

For the third and final project, in order to test how much of perception privileges the warm-cool and blue-yellow dimensions compared to their orthogonal counterparts, I compared performance of observers in a perceptual grouping task using the method of constant stimulus. Borrowing a modified paradigm from Regan and Mollon (Regan & Mollon, 1997), observers viewed an array of 0.5° circles (with magenta-green reference stimuli consistently fixed) and judged whether the stimulus pointed towards the upper left or the upper right. Individual differences in performance, where the confusion point is (i.e., where the stimulus can be judged as being in either direction), was manifest in our findings. In some conditions of the study, individual participants seem to perform worse when warm-cool and blue-yellow had had higher contrasts. The lower the contrast of the orthogonal condition is the more stable the perception is of the warm-cool and blue-yellow backgrounds. These findings corroborate earlier findings in chapters 2 and 3 that warm-cool and blue-yellow reflect a dimension of color encoding that we are most adapted to. This further begs the question as to how it is that perception privileges certain chromatic directions over others. The visual system is tuned, or at least being tuned, to chromatic directions in the environment that may be rife with warm-cool or blue-yellow hues.

These three projects, though not the entire picture, explored the nature of chromatic adaptation to a poorly understood area of perception, i.e., the warm-cool distinction of color judgement and perception. It was not until relatively recently that more and more publications and studies have come out regarding warm versus cool hues (Devinck & Knoblauch, 2024; Knoblauch et al., 2023; J. J. Koenderink et al., 2024a, 2024b; J. Koenderink & Van Doorn, 2021; Manalansan et al., 2025; Oh & Kwak, 2019, 2022). These studies further elucidated our understanding of not just warm-cool judgements, but they also advanced our understanding of the visual system and the sensitivities in color tuning the visual system may be adapted to. Further investigation is still wanting, e.g., a study into the neural mechanisms of these chromatic tuning either with neuroimaging and/or encoding models, in order to fully capture how our senses are encoded to patterns of neuronal firings.

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Chapter 2. Warm versus cool colors and their relation to color perception

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Abstract

The distinction between warm vs. cool colors is widely considered a fundamental aspect of human color experience, but whether it reflects properties of color perception or color associations remains unclear. We examined how the warm-cool division is related to perceptual landmarks of color coding and color appearance. Observers made warm-cool ratings for 36 hue angles at 3 luminance levels, and also estimated the angles for their unique (e.g. yellow or red) and binary (e.g. orange) hues. The warm-cool dimension was reliably identified by most observers, was consistent across lightness levels, and varied along an orangish-red to greenish-blue dimension that is intermediate to both the principal chromatic dimensions of early cone-opponent (cardinal) or perceptual-opponent (red-green and blue-yellow) axes. When the stimuli were projected into a uniform color space (CIELAB), a close correspondence was found between the warm-cool dimension and the perceived strength (saturation) of different hues, based on the LAB chroma. Specifically, the peak warm and cool values were hue angles with the weakest saturation, while the boundaries between the two categories corresponded to hue angles with the highest saturation. This pattern could arise if vision is selectively adapted to the spectra of warm and cool colors, and provides a potential basis for the strong but unexplained asymmetries in color coding built into perceptually uniform color spaces.

Introduction

The wavelengths of light vary continuously, but our experience of color is punctuated by prominent divisions in how we represent and categorize the spectral content of stimuli. These divisions arise at many levels, from how neural mechanisms encode color, to how we think about and interpret color. Physiologically, chromatic information is initially carried by the relative activity of the three classes of cone receptors, which absorb light with photopigments maximally sensitive to short (S), medium (M), or long (L) wavelengths of the visible spectrum. Subsequently, the signals from the cones are combined at post-receptoral stages to form a set of opponent dimensions. In the retina and lateral geniculate nucleus, the primary dimensions for color coding are given by the comparison of the L and M cones (LvsM) or signals in the S cones opposed by L and M cones (SvsLM) (Dacey, 2000; Derrington et al., 1984a). These cone-opponent dimensions are known as the “cardinal directions” of early color coding (Krauskopf et al., 1982). In visual cortex the signals from these mechanisms are further transformed into “higher-order” color mechanisms that are tuned to different directions in color space (Krauskopf et al., 1982; Lennie et al., 1990), with the tuning becoming narrower at higher stages (Kiper et al., 1997). Further transformations are likely at later levels of the visual pathway, yet how color might be represented within these later cortical stages remains poorly understood.

The principal dimensions of color experience have also been inferred by phenomenological measurements of how colors appear. In classic color-opponent theory, different hues can be represented by the perceptual dimensions of red vs. green and blue vs. yellow (Hurvich & Jameson, 1957). These dimensions differ from the cardinal axes (Krauskopf et al., 1982; Webster et al., 2000; Wuerger et al., 2005), and the neural underpinnings of the perceptual-opponent axes have yet to be resolved (Godat et al., 2024; Webster, 2020). Moreover,

it is unclear whether they have the same status or basis as the physiologically-defined dimensions. For example, the notion that a pure red or yellow sensation represents the isolated response of a red-green or blue-yellow mechanism is difficult to reconcile with the apparent population code for color in the cortex, in which any hue should stimulate multiple channels (Webster & Mollon, 1991, 1994). Further, the perceptual dimensions that appear special could reflect special properties of the environment, such as the blue-yellow variation of daylight or surfaces, rather than special states of activity in the brain (Mollon, 2006; Pokorny & Smith, 1987). These issues have raised increasing doubts about the validity of conventional color-opponent models (Bosten & Boehm, 2014; Conway et al., 2023; Webster, 2020). Nevertheless, red-green and blue-yellow are still widely considered to be fundamental dimensions of color appearance.

At still another level, colors can be classified along a wide range of dimensions that may reflect preferences, semantic correlates, or emotional impact (Elliot & Maier, 2014; Palmer & Schloss, 2010). These can include experiencing colors as light vs. heavy, active vs. passive, clean vs. dirty, or like vs. dislike (Gao et al., 2007; Ou et al., 2004). Dimensions of this kind may correspond more closely to color cognition and to the associations we make to different colors, and thus may be based on very different principles from the underlying neural and perceptual codes. For example, much of the variance in color preferences can be accounted for by the valences for the object categories people associate with different colors (e.g. blue with clear sky and water, brown with dirt or rotting fruit) (Palmer & Schloss, 2010). Yet on the other hand, sex differences in color preferences have been found to reflect different weightings of the cardinal (LvsM) mechanisms, illustrating the interplay of multiple levels in shaping color judgments (Hurlbert & Ling, 2007).

In this study, we focused on one of the most prominent yet least understood dimensions of color experience: warm vs. cool. This distinction is widely invoked in studies of the impact or

emotion of color (Ou et al., 2004), yet it is also frequently considered a fundamental dimension of color appearance (Hardin, 2000; E. Kutra et al., 2023; Koenderink & van Doorn, 2021), and has been tied to aspects of color perception ranging from neural color coding (Mollon, 1989a; I. A. Rosenthal et al., 2021) to color communication (Gibson et al., 2017; Lindsey & Brown, 2006) to salient signatures of the color environment (Rosenthal et al., 2018). The status of warm-cool judgments - and in particular the level(s) of representation to which they refer - is thus uncertain (Knoblauch et al., 2023; Koenderink & van Doorn, 2021; J. J. Koenderink et al., 2024b; Zaslavsky et al., 2019). Here we asked how warm-cool ratings align with perceptual landmarks of human color vision. While the warm-cool axis is distinct from the dimensions of cone-opponent (cardinal axes) or perceptual-opponent (unique hues) processes, the division shows a strong and surprising alignment with the relative saturation of different colors, a pattern which may reflect interactions across multiple levels of color experience.

Methods

Participants. Participants included authors JM and MW and 24 students from the University of Nevada, Reno (UNR). Participation was with informed consent and all procedures followed protocols approved by UNR's IRB.

Apparatus/Hardware. Experiments were presented on an NEC MultiSync FP2141SB CRT monitor through a Cambridge Research System ViSaGe board, which provides for high color resolution. The monitor was calibrated using a Photo Research PR 655 spectroradiometer with linearized gun outputs. Participants used a handheld keypad to record their responses.

Stimuli. The chromaticities of the stimuli were defined within a variant of the MacLeod-Boynton (D. I. MacLeod & R. M. Boynton, 1979) and Derrington-Krauskopf-Lennie (Derrington et al.,

1984a) color spaces. These spaces represent chromatic signals in terms of the two cone-opponent axes (LvsM and SvsLM) at constant luminance. The two axes were scaled so that unit distances along each axis corresponded roughly to multiples of threshold, based on previous studies (Webster & Mollon, 1994). The coordinates of the stimuli were given by:

$$LvsM = 1955*(l_{mb}-0.6568) \text{ and}$$

$$SvsLM = 5532*(s_{mb}-0.01825)$$

Where l_{mb} and s_{mb} are the coordinates in the MacLeod-Boynton diagram, and 0.6568, 0.01825 are the coordinates of the neutral gray, which had a chromaticity equivalent to Illuminant C. For the experiments the chromatic contrast was fixed at a value of 80 while the hue angle varied, with an angle of 0° corresponding to the +L pole of the LvsM axis and 90° to the +S pole of the SvsLM axis. The background had a fixed luminance of 20 cd/m^2 , while the test stimulus had a luminance of 10 cd/m^2 , 20 cd/m^2 , and 40 cd/m^2 . The stimuli were viewed binocularly from a distance of 2 m in an otherwise dark room.

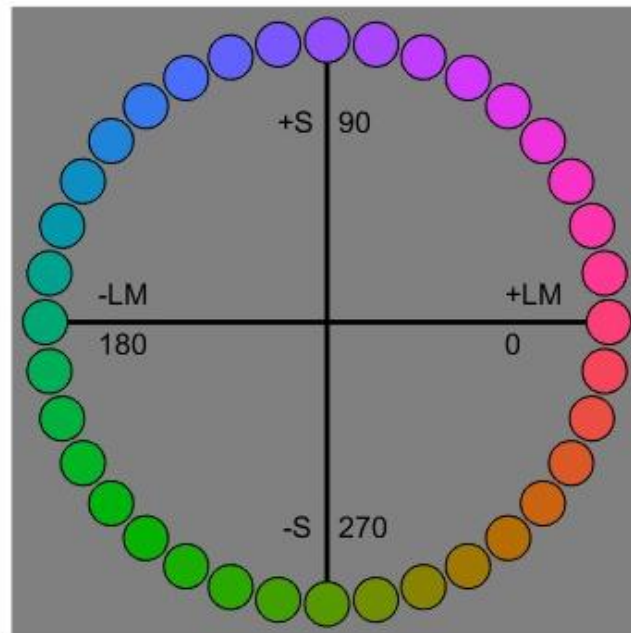


Figure 1. Color space for the experiment, defined by variations in LvsM cone or SvsLM cone signals at constant luminance. Stimuli had a fixed chromatic contrast and varied in angle relative to the neutral gray.

Procedure: warm-cool judgments. For the main experiment, colors consisted of 36 hue angles spanning the LvsM and SvsLM plane in steps of 10° (Figure 1). These were presented sequentially in random order in a uniform 2° circular field centered on the $8^\circ \times 6^\circ$ gray background corresponding to the screen size of the display (Figure 2). The stimulus was pulsed on for 500 ms with an ISI of 1500 ms and continued until a response was made, after which a new random hue angle was shown. The observer responded by using a 7-point Likert scale to rate how warm or cool the color appeared (with categories ranging from very-warm, warm, somewhat warm, neutral, somewhat cool, cool, very-cool). During the run, each hue angle was shown 4 times in random order at the same luminance level, and each session included runs at the three different luminance levels (10, 20, 40 cd/m^2), which were counterbalanced for order across observers. Reported values for individual observers are based on the average of the 4 repeated settings per condition.

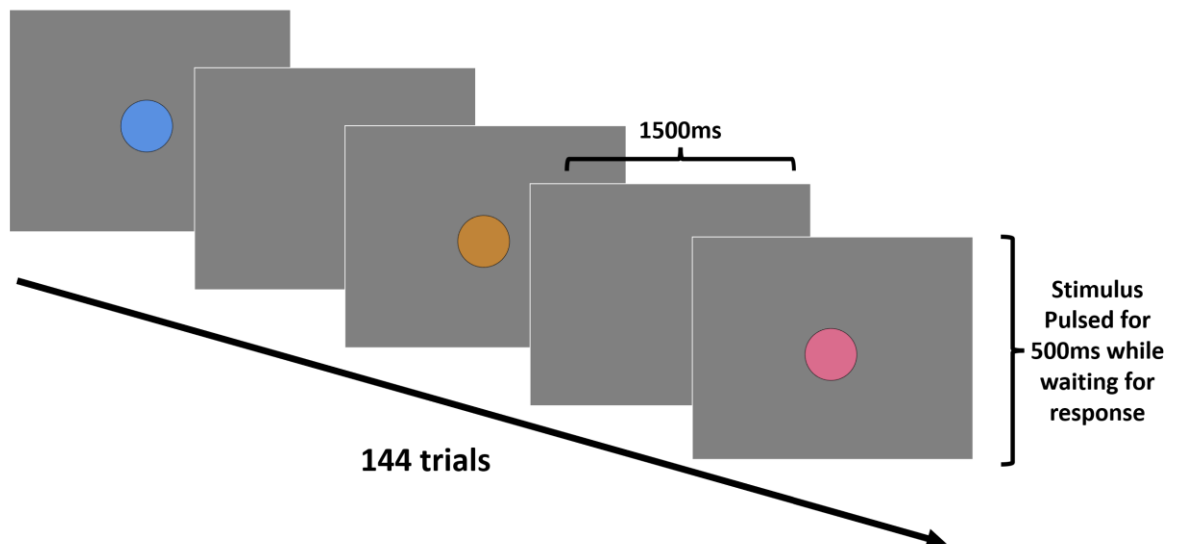


Figure 2. Experimental procedure for the warm-cool judgements. Each color was presented in random order and pulsed for 500 ms om 1500 ms off until the participant rated the warm-cool value using a 7-point scale.

Procedure: Unique and binary hues. In an ancillary experiment, for each observer we also estimated the hue angles corresponding to the unique hues (pure red, green, blue, or yellow) and binary hues (purple, cyan, yellow-green, and orange, which correspond to mixtures of the unique hues). In this case the entire set of colors was displayed on the gray background, with each circle subtending 0.75° and with a luminance of 20 cd/m^2 (Figure 3). The participant used the keypad to move a pointer clockwise (6 on the number pad) or counterclockwise (4 on the number pad) around the hue circle to indicate the angle of each hue, with the color term displayed black at the bottom of the screen. Participants were instructed to estimate the precise hue angle and not simply choose the closest example from the hues displayed. They were also instructed to locate the hues based on the null point (e.g. neither red, nor green for unique yellow or blue) or the equal balance for binary hues (e.g. equal amounts of red and yellow for orange). Prior studies have shown that unique hue judgments also correspond closely with ratings of the “best example” or focal color of each hue (Miyahara, 2003). On each run the observer made settings for each color term in random order and for 4 repetitions of each, with the cursor position randomized before each trial. Two repeated runs were made during the session, and the individual data reported are based on the mean of the 8 settings.

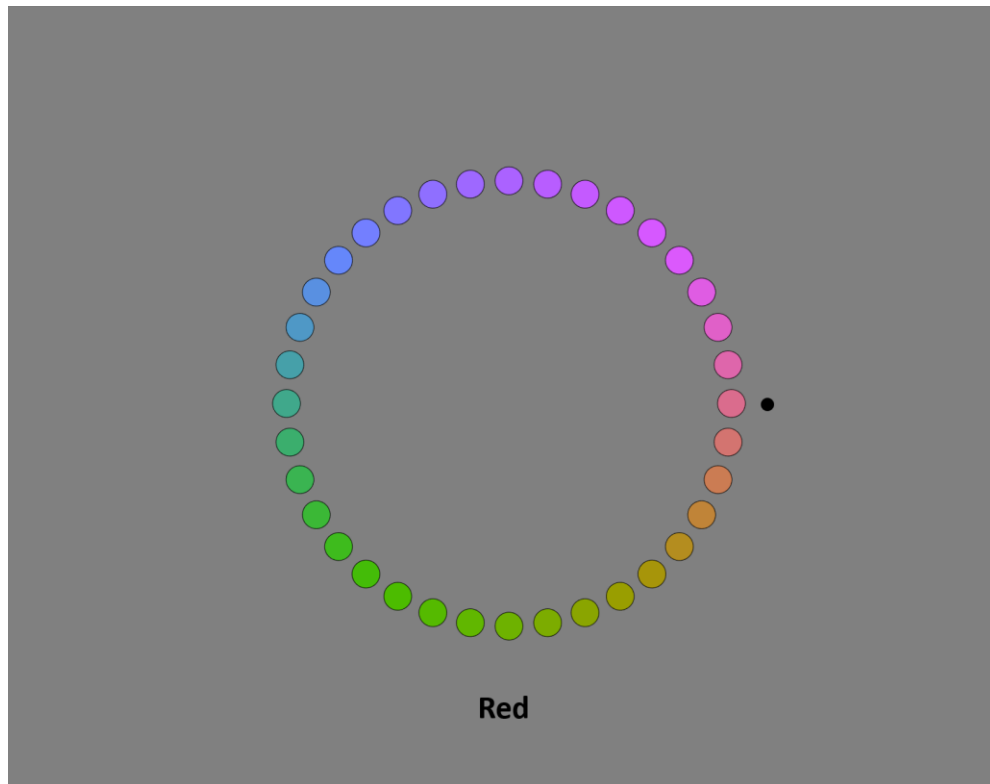
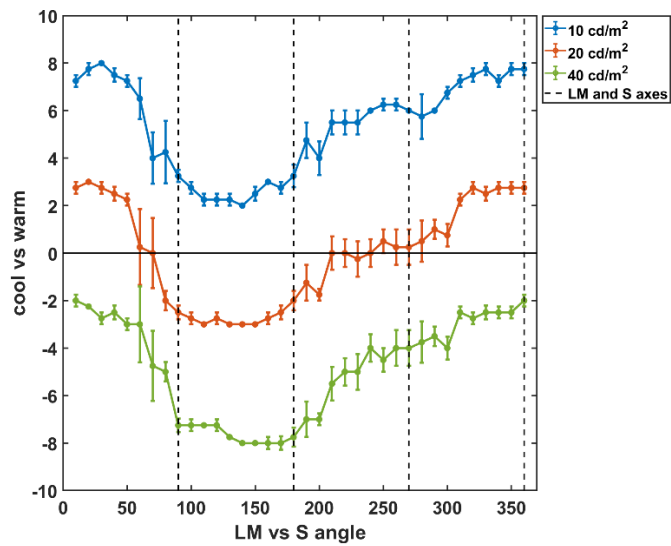
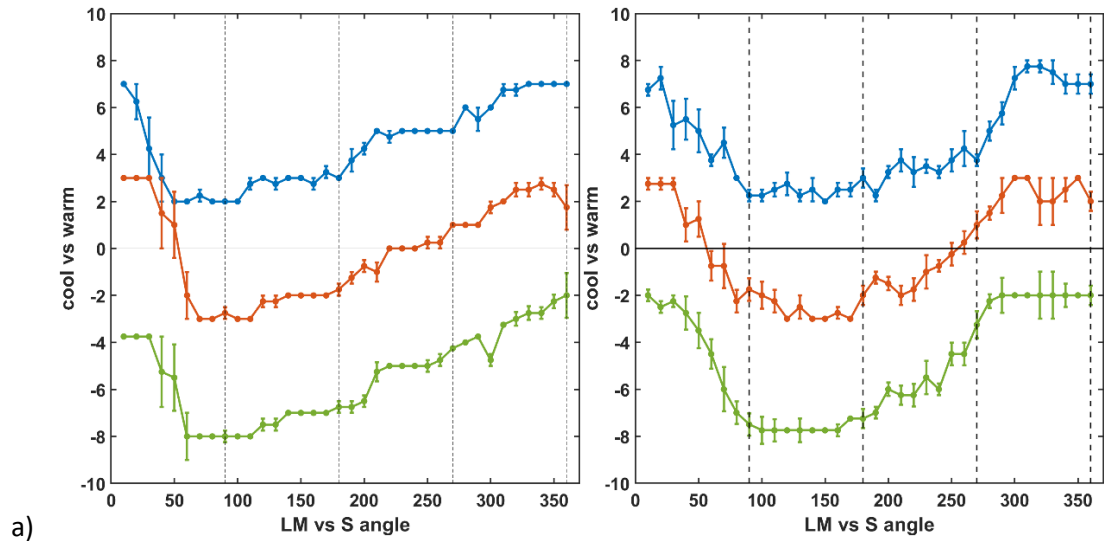


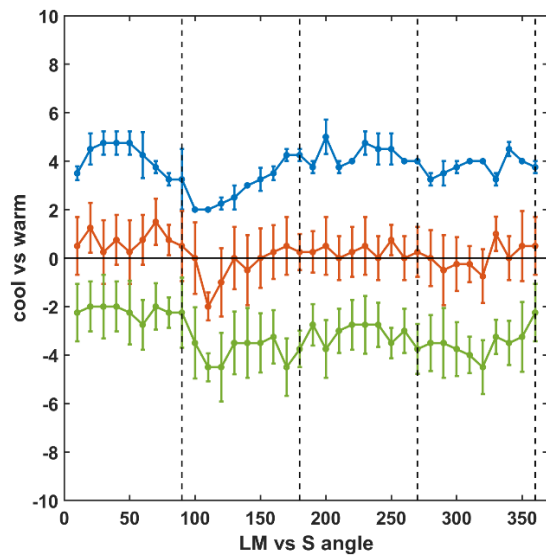
Figure 3. Illustration of the experiment for choosing unique and binary hues. The black dot was moved clockwise or counterclockwise to select the angle corresponding to the cued text (red in this example). Note participants were instructed to estimate the best angle, which could be intermediate to the displayed colors.

Results

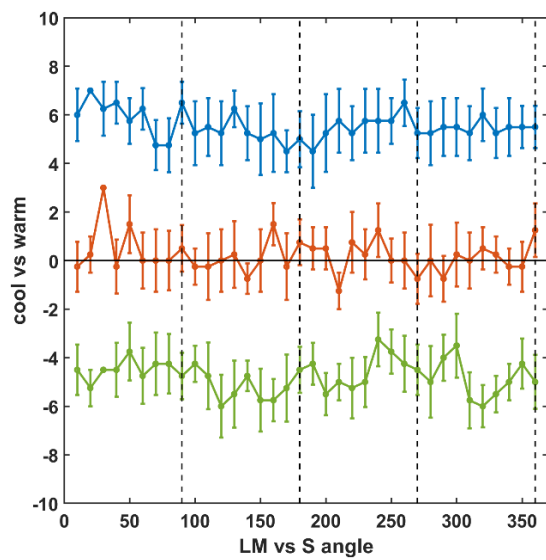
Warm-cool ratings and their relation to hue and lightness. Settings for representative individual observers and are shown in figure 4. Based on these settings, 19 of the 25 observers systematically classified the different hues consistent with a single and roughly continuous warm vs cool dimension, and were therefore included for further analyses (Figure 4 top panels). The remaining 6 were excluded because their settings showed either very low or non-systematic variation with hue, unimodal responses, or multiple apparent peaks for warm or cool (Figure 4 bottom panels). Thus, these observers were either insensitive to the warm-cool distinction or used

it to classify the hues in qualitatively different ways. Similar differences between observers have also been reported in other studies of the warm-cool dimension (Devinck & Knoblauch, in press; E. Katra et al., 2023; J. J. Koenderink et al., 2024b).





b)



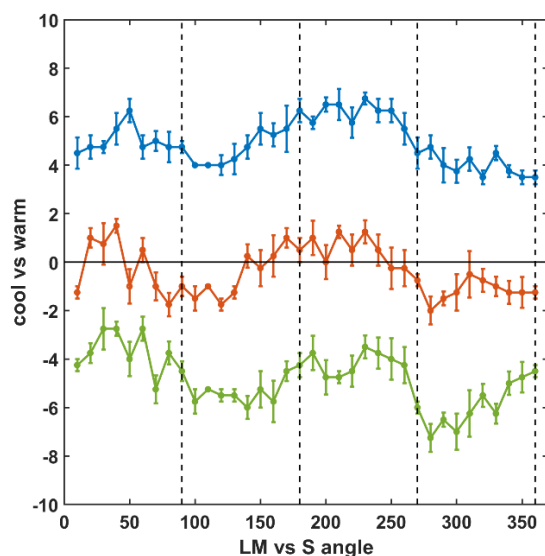
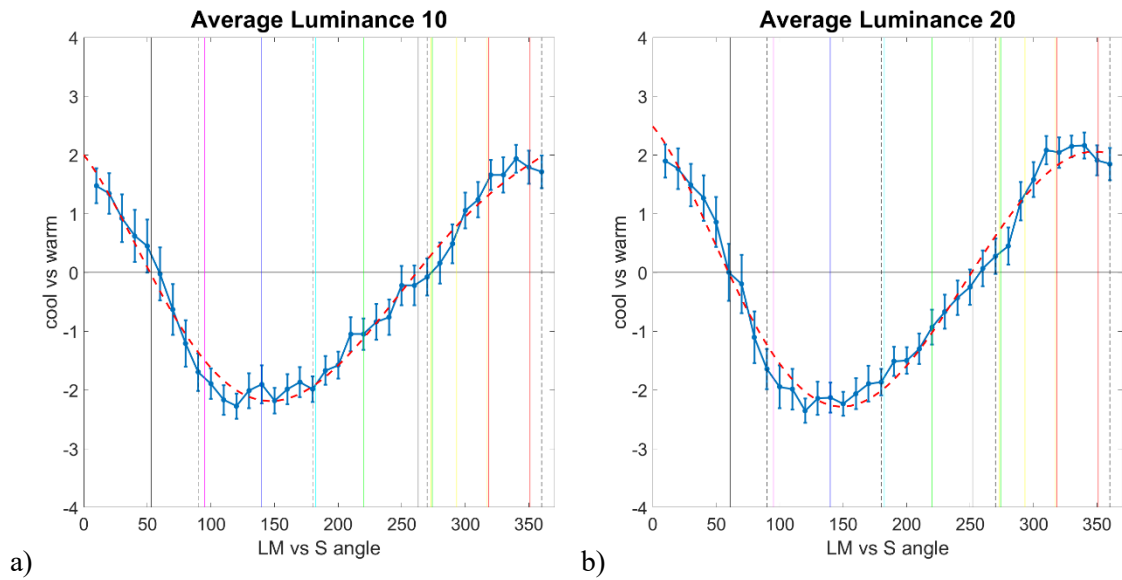
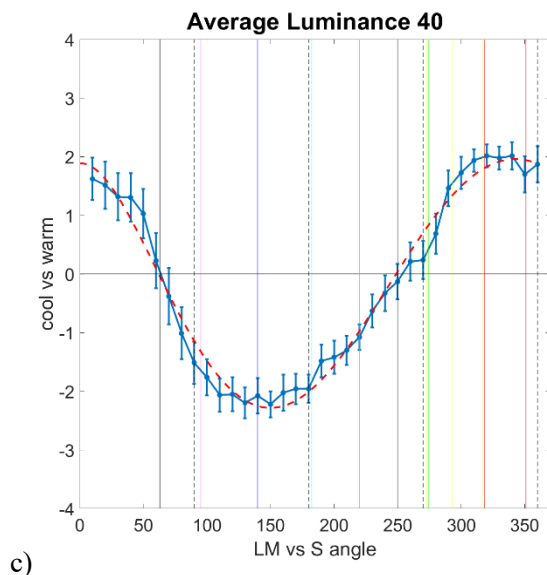


Figure 4. Representative individual ratings for warm vs. cool colors. Each panel shows the mean ratings for warm vs. cool (± 1 SEM) on a 7-point scale (-3 cool to +3 warm) as function of the stimulus angle in the LvsM and SvsLM chromatic plane. The 3 curves show the settings at each luminance level, and are arbitrarily shifted vertically by +3 (10 cd/m^2 targets), 0 (20 cd/m^2), or -3 (40 cd/m^2) for clarity. a) Top panels illustrate typical results from 3 of 19 observers whose warm-cool ratings systematically varied with chromatic angle. b) Bottom panels show results from 3 of 6 observers who were excluded from subsequent analyses because their settings did not exhibit a consistent warm-cool chromatic axis. Dashed vertical black lines show the LvsM SvsLM axes of the color space.

Figures 5a-5c plot the average functions for the 19 observers who exhibited a consistent pattern. The three panels plot the mean settings at the three lightness levels. As previous studies have found, on average the warm-cool division varies roughly from orangish-red (warm) to greenish-blue (cool) (Devinck & Knoblauch, in press; Hammond et al., 2024; E. Katra et al., 2023; Koenderink & van Doorn, 2021; J. J. Koenderink et al., 2024b). This dimension thus differs from both the cone-opponent axes (LvsM and SvsLM) and the canonical red-green and blue-yellow dimensions of color appearance. In particular, the functions are consistent with the general finding that the perceptual primaries of red and yellow are both warm colors, while the primaries blue and green are both associated with cool colors (Hardin, 2000; E. Katra et al., 2023; Knoblauch et al., 2023); though, as shown below, in our settings the warm and cool peaks were closer to red and blue than to orange and blue-green.

To estimate the actual peaks and boundaries of the functions, we fit a 5th-order polynomial to both the average settings and to each observer's individual settings, and used these to determine the angle of the zero-crossings (boundaries), or the maxima (warm peak) or minima (cool peak) of the functions. For the warm peaks the functions were phase-shifted as needed to account for the circularity of the function. As shown by the dashed lines in Figures 5a-5c, the polynomials provide a reasonable atheoretic fit to the settings.





c)

Figure 5. a-c: Average warm-cool ratings (blue solid line and points) and polynomial fit (red dashed line) for targets at the three luminance levels indicated. Points show the mean across observers ± 1 SE. Colored vertical lines represent the mean values for the 8 hue loci, dashed vertical lines represent the LM and S axes, and solid vertical lines represent the warm-cool boundaries.

Figure 6 plots the warm-cool peaks and boundaries for each of the observers (innermost points), along with the color angles selected for the unique and binary hues (see also Table 1). The three panels again show the settings for the three lightness levels tested (with the hue loci again tested only at 20 cd/m² and therefore duplicated across lightness level). These results point to the following properties of warm-cool judgments. First, the warm-cool functions were similar across the different lightness levels. This is consistent with previous findings of Katra et al., though two recent studies have found some effects of lightness on the judgments (Devinck & Knoblauch, in press; Hammond et al., 2024).

Second, there are large individual differences in both the warm-cool functions and the observers' selections for the color terms. This inter-observer variability is a consistent finding in studies of color appearance, though the basis for it remains poorly understood (Emery et al., 2023; Emery & Webster, 2019; Kuehni, 2004; Lindsey & Brown, 2006, 2009; Webster et al.,

2000). The variations in the warm-cool settings were highly consistent across lightness levels. Correlations between across the three luminances averaged 0.93 for the warm peaks and 0.89 for the cool peaks, and were also strong for the warm-cool boundary in the “purple” direction ($\sim 60^\circ$), or WC boundary 1 (averaging 0.84); though they were generally weak for the second WC boundary in the “yellowish-green” direction ($\sim 260^\circ$) (see Table 2). These high correlations suggest that that the differences between observers were reliable.

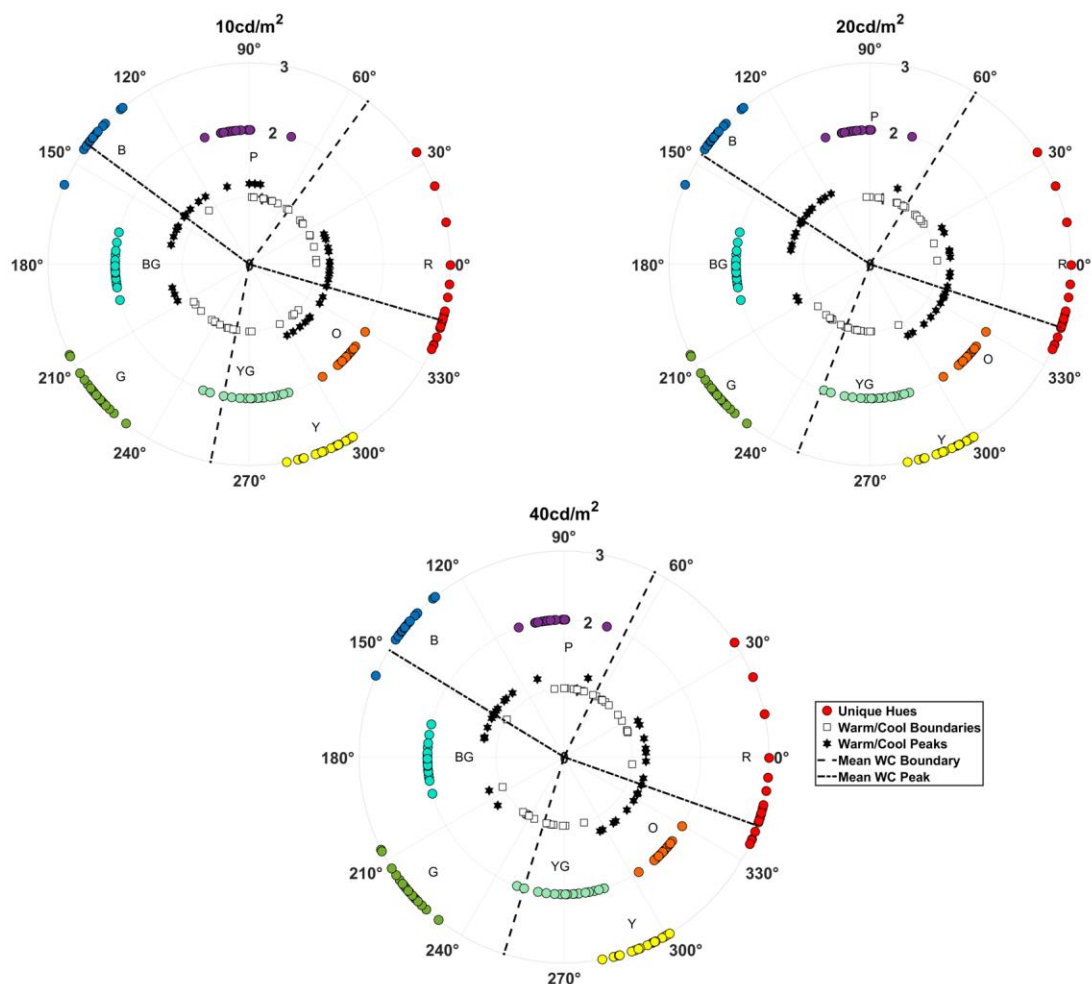


Figure 6. Individual warm-cool boundaries (unfilled symbols, innermost radii) or peaks (second radii), compared to the focal choices for the unique and binary hues, as indicated by the category labels. Dashed lines indicate the average angles for the warm-cool peaks (small dashes) and boundaries (large dashes). The three panels show the settings for the three lightness levels. Note

unique and binary hue settings were only collected at 20 cd/m² and are repeated across the panels.

Table 1: mean angle and variance of the warm-cool peaks and boundaries and of the 8 hue loci

	10 cd/m ²	20 cd/m ²	40 cd/m ²
	$\mu \pm \sigma$	$\mu \pm \sigma$	$\mu \pm \sigma$
warm	343.7 \pm 27.4	341.7 \pm 25.3	340.5 \pm 27.6
cool	143.5 \pm 36.1	146.9 \pm 30.5	148.7 \pm 30.2
boundary 1	53.9 \pm 32.1	58.4 \pm 24.3	63.7 \pm 31.2
Boundary 2	258.9 \pm 31.3	249.1 \pm 18.7	252.9 \pm 30.4
yellow		292.7 \pm 5.7	
blue		139.9 \pm 5.9	
green		220.2 \pm 6.5	
red		350.2 \pm 16.1	
blue-green		181.8 \pm 6.9	
orange		316.1 \pm 5.5	
purple		95.5 \pm 7.6	
yellow-green		272.1 \pm 10.3	

Table 2: correlations between the same warm-cool peaks or boundaries across the three luminance levels. Corrections for multiple comparisons here and elsewhere are based on the Benjamini-Hochberg procedure for controlling the false discovery rate.

	10 vs 20 cd/m²	10 vs 40 cd/m²	20 vs 40 cd/m²
warm peak	0.91*	0.95*	0.94*
cool peak	0.89*	0.82*	0.96*
WC boundary 1	0.79*	0.96*	0.76*
WC boundary 2	0.84*	0.22	0.30
*p <= 0.05 corrected for multiple comparisons			

Table 3: correlations between warm-cool peaks or boundaries at each luminance level.

	10 cd/m²	20 cd/m²	40 cd/m²
warm vs cool	0.50	0.41	0.23
warm vs boundary 1	0.59*	0.83*	0.51
warm vs boundary 2	0.20	0.23	-0.24
cool vs boundary 1	0.64*	0.49	0.67*
cool vs boundary 2	0.48	0.73*	0.36
boundary 1 vs 2	-0.07	0.13	-.07
*p <= 0.05 corrected for multiple comparisons			

Table 4: Correlations between the warm-cool loci and hue loci at 20 cd/m².

<i>Luminance 20 cd/m²</i>								
	R	P	B	BG	G	YG	Y	O
R	1							
P	-0.02	1						
B	0.06	-0.06	1					
BG	-0.18	-0.15	0.04	1				
G	-0.20	-0.17	-0.23	0.10	1			
YG	-0.47	-0.13	0.10	-0.01	0.53	1		
Y	0.05	0.16	0.06	-0.14	0.04	0.14	1	
O	-0.34	-0.40	-0.08	0.32	-0.01	0.14	-0.38	1
WC 1	0.46	-0.13	-0.20	-0.09	-0.20	-0.46	0.31	-0.54
WC 2	0.23	0.19	0.11	-0.61	-0.27	-0.05	0.26	-0.12
Warm	0.30	-0.11	-0.07	-0.24	-0.42	-0.48	0.37	-0.31
Cool	0.31	-0.04	-0.12	-0.40	-0.15	-0.12	0.20	-0.22

*p<0.05 corrected for multiple comparisons

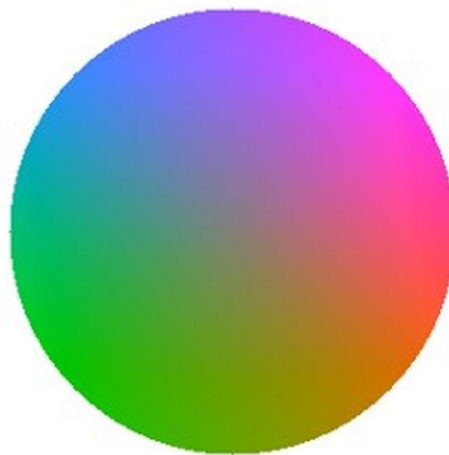
In contrast, at each lightness level the variations in the peaks and boundaries tended to vary independently of each other (Table 3), and also varied largely independently of observers' hue foci, which - as also found previously (Emery et al., 2023; Webster et al., 2000) – were themselves not strongly correlated even for adjacent color categories (Table 4). In the case of the warm-cool dimension, there was a trend for the warm or cool peaks to covary with the purplish warm-cool boundary, but the correlations between warm and cool, or between the two boundaries, were not themselves significant. The average warm and cool peaks also did not

significantly differ from the mean settings for red and blue respectively ($t(18) \leq 1.32$, $p \geq 0.20$), but were nevertheless uncorrelated with them. Taken together, these results suggest that the warm-cool dimension is distinct from other color categories, and moreover that the dimension itself does not reflect a single underlying process (since warm and cool tended to vary independently). This is again similar to the findings for red-green and blue-yellow dimensions of color appearance, for which the opposing primaries also vary independently and thus are not yoked as part of a common opponent mechanism (Emery et al., 2023; Webster et al., 2000).

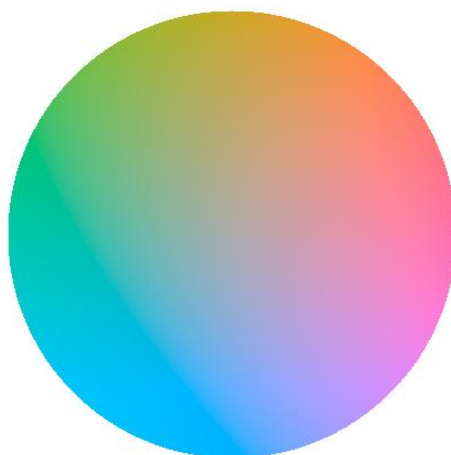
Finally, the results also indicate that the warm-cool dimension is not aligned with the LvsM and SvsLM cardinal axes. In particular, at each lightness level the peaks of the function were significantly different from the cardinal axes, again with warm rotated toward orange relative to the +LM pole and cool rotated toward blue for the -LM pole (all $t(18) \geq 2.59$, $p \leq 0.018$). Similarly, the boundaries at each lightness were also significantly shifted toward red relative to the +S pole and toward green relative to the -S pole ($t(18) > 2.44$, $p \leq 0.025$), with the exception of the yellowish-green boundary at the 40 cd/m² luminance, which was not significant ($t(18) = 1.54$, $p = 0.14$). Moreover, while variations in the angles of the cardinal axes occur because of variations in spectral sensitivity, these are generally too small to account for variations in color appearance, and also predict highly correlated changes across the opposite poles (Simoncelli & Webster, 2024; Webster et al., 2000), which again was not observed.

Warm-cool ratings and their relation to saturation. To further explore the nature of warm-cool judgments, we next examined how they depended on the saturation of the different hues tested. The stimuli we sampled all had equal chromatic contrast as defined by distance from the neutral gray in the cone-opponent plane (as defined by our scaling metric). However, these distances do not necessarily have equal “perceived” chromatic contrast, or saturation. To explore this factor, we re-examined the settings within a different color space designed to capture the perceptual

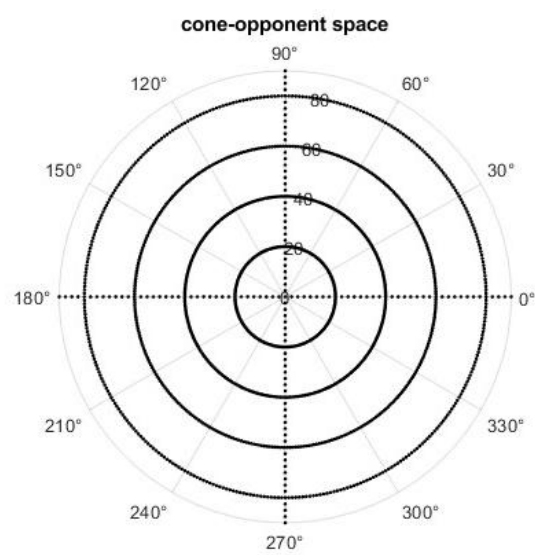
differences between colors rather than the cone-opponent signals defining the stimuli. For this we projected the set of stimuli into the 1976 CIELAB uniform color space, which is a standard space for evaluating perceptual color differences (Luo, 2023). Such uniform color spaces apply nonlinear transformations of the color coordinates so that distances within the space (known as ΔE) denote the magnitude of perceptual differences. All such uniform color spaces are known to provide only an approximation to perception, but capture general and common properties of perceptual scaling. For example, the CIELAB representation was designed to be similar to the perceptual scaling of color predicted by the Munsell Color System, which is also a widely used and empirically-based system for assessing color appearance and perceptual differences (Robertson, 1977).



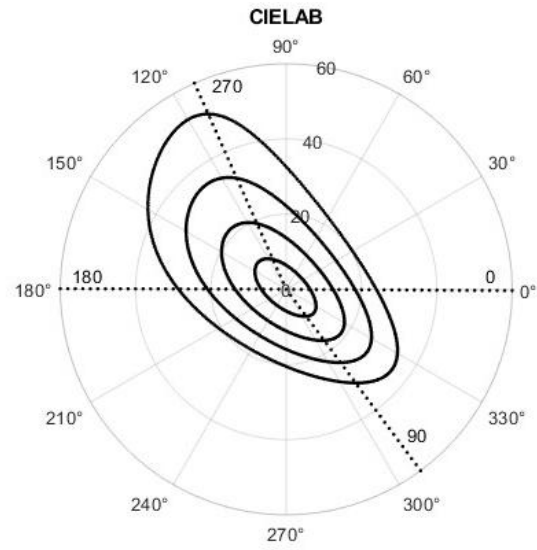
a)



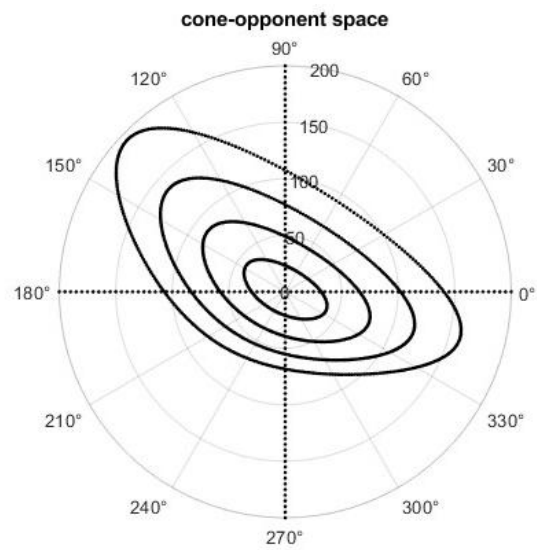
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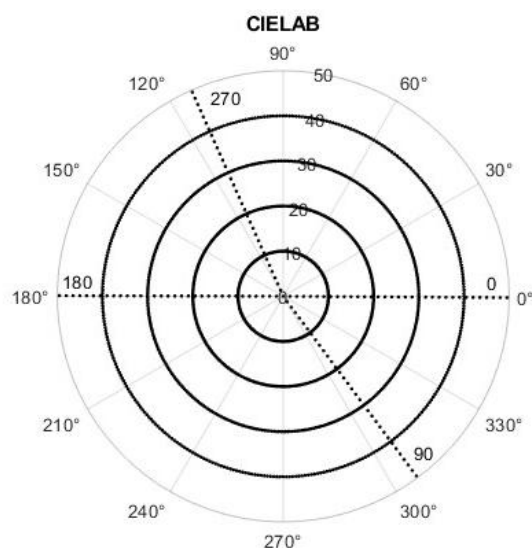
c)



d)



e)



f)

Figure 7. Comparisons of equivalent stimulus contours in spaces defined by cone-opponent signals (a, c, and e) or scaled for perceptual strength (in CIELAB, b, d, and f). Signals with constant cone-opponent contrast (c) project to stimuli with different predicted saturation (d), and vice versa, so that constant CIELAB chroma (f) project to distorted cone-opponent contrasts (e). Dashed lines in all figures represent the cardinal directions in the cone-opponent plane. Note that our version of the cone-opponent space follows the MacLeod-Boynton diagram in plotting the S (90°-270°) axis as increasing S signals, which is inverted in the CIELAB space.

Figure 7 illustrates the relationship between stimuli in the cone-opponent and CIELAB spaces. The images at the top depict the location of different hues within each space. Contours with uniform cone-opponent contrast (Figure 7a, as in our stimulus set) project to distorted contours in CIELAB (Figure 7b) with points closer to the CIELAB origin corresponding to weaker (lower chroma or less saturated) stimuli. Conversely, contours with constant chroma in the CIELAB (Figure 7d) require different magnitudes of cone-opponent contrast for different hues, and thus again project to distorted contours in the cone-opponent diagram (so that the weakest hues require larger cone contrasts for the same perceptual magnitude; Figure 7c).

Figure 8 shows the cone-opponent contour we sampled for the three lightness levels and their projection into CIELAB. For each we estimated the maxima and minima of the projected contours (shown by the red symbols in the figure), and compared these to the warm and cool

peaks and boundaries based on the fits to the average warm-cool functions (shown by the orange, cyan, and gray symbols respectively, in the figures). This analysis reveals a striking correspondence between the orientation of the warm-cool dimension and the orientation of constant saturation within the cone-opponent space.

This is further shown in the scatterplot in Figure 9, which plots the absolute difference between the warm-cool or hue settings versus the four maxima and minima in the projected contours (all for the luminance of 20 cd/m²). This compares the warm-cool peaks and boundaries to the maxima and minima in the predicted saturation (see also Table 4). In each case, the warm-cool peaks or boundaries fall very close to the maximum or minimum values in the contours. In contrast, all of the hue foci were significantly different from the contour extrema ($t(18) \geq 2.73$, $p \geq 0.014$) with the exception of unique blue ($t(18) = 1.26$, $p = 0.22$), which was similar in angle to the cool peak.

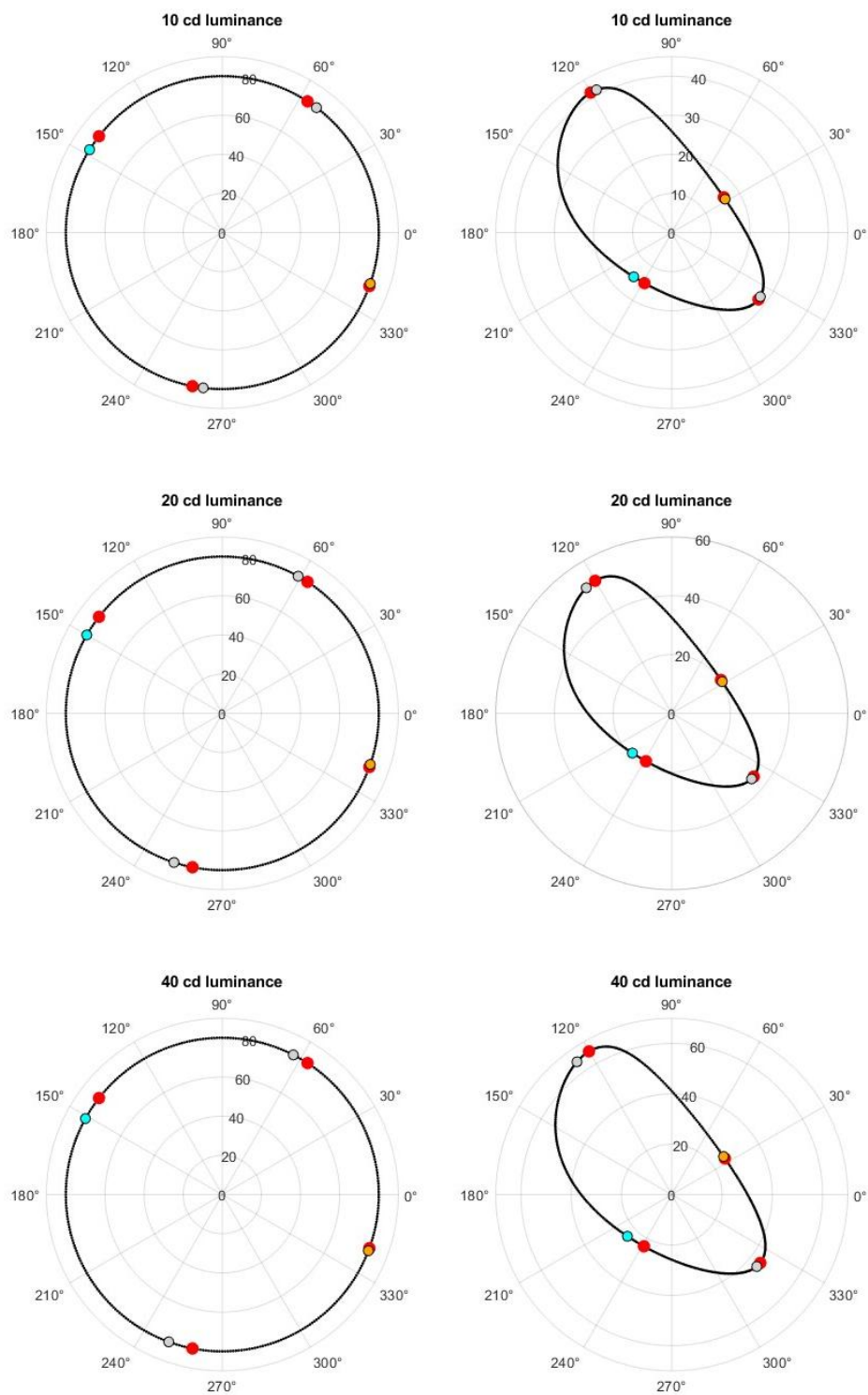


Figure 8. Stimulus sets in the cone-opponent space (left panels) or CIELAB uniform color space (right panels), for the three lightness levels tested. Each panel compares the warm peak (orange),

cool peak (cyan), or warm-cool boundaries (gray) to the maxima and minima of the saturation for the constant cone-opponent contrasts in the uniform color space (red).

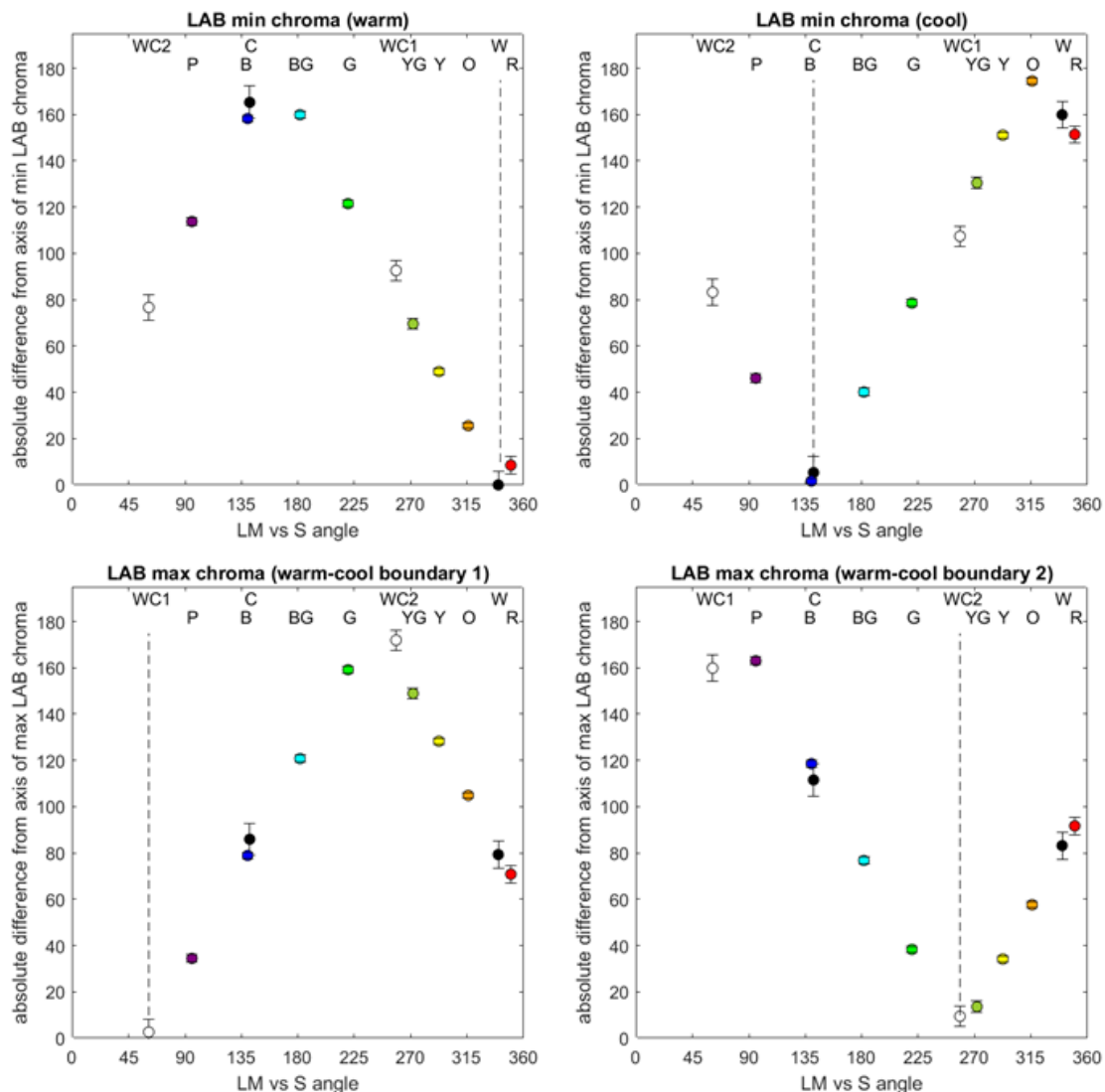


Figure 9. Correspondence between the warm-cool or hue loci and the saturation maxima and minima predicted by the CIELAB chroma of the stimuli. Symbols plot the absolute angular difference between each measured hue angle (given by the labels at the top of each panel) and the angles of each of the 4 extrema of the LAB contours (shown by the dashed vertical lines. Error bars are ± 1 SEM.

A further important feature of this association is that the hues that are strongest in the warm-cool dimension are in fact the weakest in saturation – i.e. the warm-cool peaks correspond to the minima in saturation contours, while the boundaries correspond to the maxima. Notably,

these associations would not be apparent if stimuli were analyzed within either color space alone, but are instead revealed by the relationship between the physiological cone-opponent contrasts and their perceptual strength as predicted by standard uniform color spaces.

These saturation loci and our finding that they closely track the warm-cool dimension can provide a useful heuristic for predicting the “heat” of colors, something that is of wide interest in color applications (Ou et al., 2004). To construct this, we estimated the cone-opponent maxima and minima over a range of constant-chroma values within the LAB space, and then fit these as a function of the A and B color coordinates of the stimulus. The contours are depicted in Figure 10, along with the warm-cool dimension modeled by Ou et al. (Ou et al., 2004), which represents a simple linear axis in LAB along an axis of 50°. The dimension based on the saturation contours predicts a roughly similar direction in the color plane, but is a strongly curved. By this account, the equations for predicting the warm-cool axes and strength for a given A-B coordinate are:

$$\text{warm-cool axis } A = 1.0674B + 0.0396B^2 + 0.000565B^3$$

$$\text{warm-cool boundary: } A = -1.0996B + 0.0104B^2$$

$$\text{warm-cool strength: } S_{wc} = 0.6792A + 0.7233B + 0.0013A^2 + 0.0042AB + 0.0044B^2$$

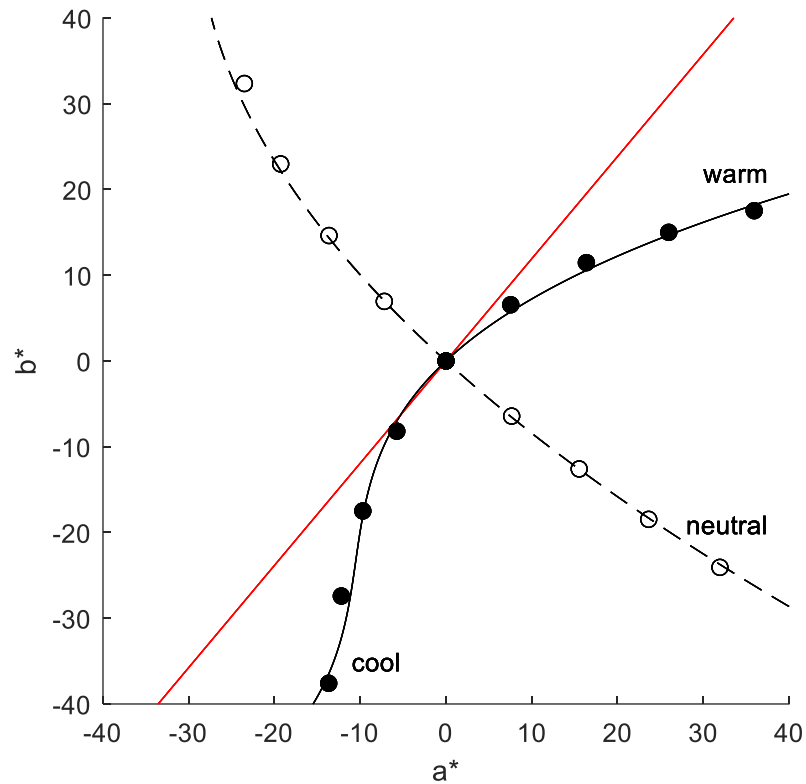


Figure 10. Predicted warm-cool axis (solid black line) and boundary (dashed line) from the minima (filled symbols) and maxima (unfilled symbols) of iso cone-opponent contrast contours within the CIELAB space. Solid red line plots the warm-cool dimension estimated by Ou et al. (Ou et al., 2004).

Discussion

As noted, the notion of warm vs. cool colors has been central to discussions of color experience at many levels, ranging from principles of color appearance to art to the philosophy of color (Hardin, 2000; E. Kutra et al., 2023; Knoblauch et al., 2023; Koenderink & van Doorn, 2021; J. J. Koenderink et al., 2024a, 2024b; Levine, 1991; Ou et al., 2004; Palmer, 1999; Unwin, 2012). Many previous studies have measured warm-cool scales for stimuli, and our results are largely consistent with these in showing that the dimension encompasses red and yellow as warm

colors and blue and green as cool, a partition that is intermediate to both the cardinal LvsM and SvsLM axes of early cone-opponent coding, and to the red-green and blue-yellow axes of color appearance (Hardin, 2000; E. Katra et al., 2023; Knoblauch et al., 2023). The idea that it represents a distinct dimension is further suggested by our findings that individual variations in the warm-cool settings were independent of variations in focal color choices. This suggests that there may be only a weak link between the warm-cool foci and specific hues. Moreover, as with different hue categories, we also found that the warm and cool foci were themselves uncorrelated. Again, this was despite the fact that warm-cool loci remained very consistent across the different lightness levels, indicating that the interobserver variations in the settings were highly reliable relative to the within-observer settings. This suggests that it may be inaccurate to characterize warm and cool as two poles of a single underlying opponent dimension, just as red and green (or blue and yellow) do not appear strongly tied to a unitary opponent process (Emery et al., 2023; Webster et al., 2000). Instead, warm and cool colors may reflect two largely complementary yet independent categories. But what do these categories represent?

In the World Color Survey, a monumental study of color naming patterns across 110 languages (Kay et al., 2009), some languages have been shown to classify all colors with only two basic color terms that group colors roughly in terms of a warm-cool divide, and Kay and McDaniell therefore suggested that this division could be the earliest stage in the evolution of linguistic color categories (Kay & Maffi, 1999; Kay & McDaniell). This superordinate dimension has also been found in statistical analyses of the naming patterns within the World Color Survey. When these patterns are limited to two clusters, the responses across languages divide in terms of a warm-color dimension, and the lowest concordance in naming are for stimuli near the warm-cool boundary, suggesting that stimuli on either side of the boundary are treated as distinct (Lindsey & Brown, 2006). Consistent with this evidence for warm vs. cool categories, Holmes

and Regier also found categorical perception along the warm-cool dimension, such that within category stimuli (e.g. two warm colors) were less distinct than stimuli that spanned the category boundary (Holmes & Regier, 2017).

Such studies reveal the prominence of potential warm and cool categories but leave open the question of their basis. However, more recently, color naming patterns have also been analyzed in terms of the information they communicate (Jameson, 2005). Across languages with varying numbers of basic color terms, the terms associated with warm colors are communicated more efficiently (Gibson et al., 2017; Lindsey et al., 2015). Analyses of the chromatic information in images has also found that warm colors are more strongly associated with objects while cool colors are more likely to be tied to the image background (Gibson et al., 2017; Rosenthal et al., 2018). This raises the possibility that the warm-cool dimension may be superordinate because it reflects a basic distinction between the relevance of color-associated information in scenes, though the warm-cool asymmetry may also reflect asymmetries in the structure of perceptual color space (Zaslavsky et al., 2019).

The link of warm and cool with scene color statistics could provide a potential account for our primary finding - that the warm-cool categories closely track the relative saturation of hues that are matched for equivalent cone-opponent contrasts (based on their relative chroma in CIELAB). Recall again that this relation was such that the hues that are most prototypical in terms of the warm or cool attribute reflect colors that are predicted to be weakest in saturation. While this seems paradoxical for color categories, it is in fact consistent with the idea that color vision (like most if not all sensory processes) adapts to the gamut of stimuli the observer is exposed to (von der Twer & MacLeod, 2001; Webster, 1996; Webster, 2014, 2015; Webster & Mollon, 1997). For example, natural daylight - and the color gamuts of many natural scenes – tend to vary most along a bluish-yellowish dimension, and in turn, sensitivity to this dimension

tends to be weaker (Bosten et al., 2015; Goddard et al., 2010a; Skelton et al., 2023; Skelton et al., 2024; Webster & Mollon, 1997). This has been explained by adaptation processes that match sensitivity to the stimulus range, so that the range of available neural responses remains optimized (Laughlin, 1981; von der Twer & MacLeod, 2001). Uniform color spaces might embody these long-term adaptations – so that the distortions in the relative perceptual salience of different hues (as illustrated in Figures 7 and 8) are inversely related to the strength of the corresponding color signals in the environment.

However, a conundrum has been that the biases in natural scene statistics do not in fact closely align with the biases predicted by uniform color metrics (K. C. McDermott & M. A. Webster, 2012). Specifically, the principal axes of natural color gamuts tend to be along bluish-yellowish axes for panoramic or arid scenes (Webster & Mollon, 1997), while for scenes dominated by foliage, the distributions instead are biased toward the SvsLM cone-opponent dimension (i.e. toward greenish-yellow axes) (Regan et al., 2001; D. L. Ruderman et al., 1998; Sumner & Mollon, 2000). In contrast, the saturation biases implicit in uniform color spaces are instead rotated toward orange and red (i.e. closer to the LvsM dimension). Thus by this account the salience of colors predicted by uniform color metrics has remained perplexing (K. C. McDermott & M. A. Webster, 2012).

The present results suggest a resolution to this discrepancy. The finding that the predicted salience corresponds closely to the warm-cool dimension – and that warm-cool colors correspond to a selective loss in perceived contrast along this dimension – suggests the possibility that visual coding is somehow adapted to the color variations along this dimension, rather than the more greenish-yellow biases found in the gamut of typical natural color distributions. One way this could occur is because global color statistics – on which most color statistics are based - do not take into account how observers visually sample scenes, and the colors that are most important to

attend to, such as the diagnostic colors of objects (Gibson et al., 2017). It may also be that the color distributions that humans in modern societies are adapted to are in fact unnatural, because they include fabricated colors in which reddish and orangish hues are likely far more prevalent than in typical natural scenes of forests and savannahs. Finally, most measures of the color statistics of scenes are for daylight and under-represent the reddish-orange lighting at dawn or dusk, which may have disproportionate influence on behavior (Dominy & Melin, 2020). Future studies might explore these questions by directly measuring the visual diet of modern environments as actually sampled by observers (Greene et al., 2024), and recently we explored the visual salience of the warm-cool axis by using a color search task (Manalansan et al., in press). This showed the warm-cool targets are less conspicuous compared to the orthogonal (~warm-cool boundary) axis, but similar biases were also found for the blue-yellow axis. In any case, the current results suggest that the warm-cool dimension is not merely a conceptual construct, but is tied to a prominent yet largely hidden and previously unexplained asymmetry in the perceptual processing of color, and one which might arise from and shed further light on how color appearance is shaped by the color environment.

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Chapter 3. Visual search for warm and cool colors

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Abstract

Warm vs cool colors are considered a fundamental aspect of color experience, yet the basis for this distinction remains poorly understood. Recently we found that the warm-cool dimension closely aligns with sensitivity biases implicit in uniform color spaces (Manalansan and Webster, *Journal of Vision* 2023), which predicts that color vision is less sensitive to the warm-cool axis than other chromatic axes. Here we tested this prediction by measuring visual search for color targets on backgrounds defined by different axes in color space. The search task involved locating a circular chromatic target sampled from a range of chromaticities that was presented on a background of ellipses that randomly varied in color along the warm-cool (roughly orange-cyan) axis, a blue-yellow axis, or along magenta-greenish axes were perpendicular to the warm-cool or blue-yellow axis. Search times were faster on both warm-cool and blue-yellow backgrounds than the orthogonal backgrounds. However, there was not a difference between these two axes, or for warm vs. cool hues or blue vs. yellow hues. These results are consistent with weaker sensitivity for the warm-cool and blue-yellow axes of color space, but do not reveal a salience difference between colors more strongly associated with objects and surfaces (warm and yellow) versus backgrounds and illumination (cool and blue).

Introduction

Colors can be distinguished along many dimensions, from physiologically based (e.g. the cardinal cone-opponent dimensions of retinal color coding), to perceptually based (e.g. the red-green and blue-yellow dimensions of Hering's opponent process theory), to associative or affective judgments (e.g. light vs heavy, clean vs dirty, like vs dislike). One of the most prominent and widely invoked distinctions is between warm vs. cool colors. However, this dimension is also one of the most poorly understood. In particular, it is not clear whether warm vs. cool directly reflects the sensory representation of color (Rosenthal et al., 2021) or is a learned association to properties of the world (Ho et al., 2014) or whether it reflects a combination of these factors (Koenderink & Van Doorn, 2021). Despite this, observers can reliably judge the warm-cool attribute of color (Devinck & Knoblauch; Hammond et al., 2024; Katra et al., 2023; Manalansan et al., 2024) (though not as reliably as dimensions such as red-green or blue-yellow) (Koenderink et al., 2024), and these judgements seem to remain relatively stable across cultures (Ou et al., 2004; Ou et al., 2012).

In previous studies, we found that warm versus cool judgements align with asymmetries in color coding that are implicit in uniform color spaces, which are designed to represent equal perceptual differences by equal distances within the space (Manalansan & Webster, 2023; McDermott & Webster, 2012). In particular, hue angles that were rated as the most warm or cool corresponded to directions in a cone-opponent space that required the highest contrast to yield an equivalent chroma in the perceptually uniform metric (CIELAB) (Manalansan & Webster, 2023). This suggests that the maxima of the warm-cool dimension correspond to hues to which we are predicted to be the *least* sensitive. Conversely, hues that were rated as the boundaries between

warm and cool required the weakest cone contrasts to yield the same chroma, and thus are the hues that uniform spaces predict our color vision is *most* sensitive to.

The basis for this correspondence is unclear. The reduced sensitivity to the warm-cool dimension could arise if this is the dominant axis of variation in the color environment, so that observers are more strongly adapted to these colors (McDermott & Webster, 2012). Color biases can in fact be very strong in natural color gamuts (Webster & Mollon, 1997). However, the warm-cool dimension varies from orange to cyan (Devinck & Knoblauch; Elan Katra et al., 2023; Koenderink & Van Doorn, 2021; Manalansan et al., 2024), while measurements of natural images instead tend to vary along a blue-yellow dimension (Ruderman et al., 1998; Skelton et al., 2024; Webster et al., 2007; Webster & Mollon, 1997). Consistent with this, many different studies have found that visual sensitivity is reduced along the blue-yellow dimension. This includes measures of threshold sensitivity (Bosten et al., 2015; Boynton et al., 1986; Skelton et al., 2024), visual salience (McDermott et al., 2010), visual discomfort (Juricevic et al., 2010), and neural responses for color (Goddard et al., 2010b), and these blue-yellow biases appear to arise as early as four months of age (Skelton et al., 2023). Thus, there is a potential discrepancy between the sensitivity biases predicted by scene statistics and different perceptual tasks on the one hand, and by warm-cool and the biases predicted by uniform color spaces on the other (McDermott & Webster, 2012). However, in many of these perceptual tasks, the sensitivity to different chromatic directions was sampled only coarsely, so that it remains unclear whether the sensitivity bias is aligned more closely with blue-yellow or warm-cool, or whether it reflects a broadly tuned bias affecting both axes similarly.

In this study, our first goal was to examine the relative salience of signals along the warm-cool or blue-yellow axis, and compare both to color salience along orthogonal color directions. We use salience to refer to how conspicuous a color appears, which depends on how

different the color is from its background, as well as how sensitive observers are to these differences. For example, a red target will not be salient on a background of red and green colors, but should be highly conspicuous on a background of blue and yellow colors. Moreover, if observers are less (or more) sensitive to the background colors, then colors that differ from this background should be more (or less) salient or conspicuous. To examine this, we used a visual search task similar to the paradigm developed by McDermott et al. 2010, where observers searched for color targets superimposed on a dense background of colors, simulating a “foraging” task of finding a fruit among foliage. Their study showed that it was easier to detect colors that differed from a blue-yellow background than for the orthogonal magenta-green background. This is again consistent with weaker sensitivity to the blue-yellow axis, so that colors that differ from this axis stand out better or are more salient. Our goal was to compare these results with targets and backgrounds that instead varied relative to the warm-cool axis.

A second goal of our study was to test for potential differences in the salience of warm versus cool, or blue versus yellow colors. Analyses of color in images have found that warm colors tend to be associated with objects while cool colors are more likely to correspond to backgrounds (Conway et al., 2020). Cortical regions sensitive to color also exhibit a “warm” bias (Pennock et al., 2023). Similarly, there are asymmetries between bluish versus yellowish hues. Bluish hues tend to be more strongly discounted and are more likely to be attributed to lighting or shading (Churma, 1994; Hurlbert, 2019; Pearce et al., 2014; Winkler et al., 2015), while yellowish hues are more likely to be attributed to surface reflectance (Winkler et al., 2015). Thus, both yellow and warm hues potentially signal more ecologically relevant information which might increase salience or attention in a color search task, possibly similar to the way that pink hues have been found to be more readily detected in color search (Lindsey et al., 2010). To examine these questions, we also compared search performance both on backgrounds defined by

a single chromatic axis (e.g. blue-yellow) and on backgrounds that included many chromatic directions (at a constant chromatic contrast).

Methods

Participants. Participants included authors JM and CS along with 12 students who were unaware of the specific aims of the study. The students were recruited from the University of Nevada, Reno (UNR), and different subsets of observers participated in the single-axis background condition ($n=11$) or the backgrounds with all hues ($n=6$). Participation in, and procedures of, the study were conducted with informed consent following UNR's IRB protocols and consistent with the Declaration of Helsinki. Observers self-reported normal color vision but were not formally assessed. However, typical color losses would manifest as elevated reaction times along the LvsM chromatic axis (Vanston et al., 2021), which was not observed for any of the participants.

Apparatus and Hardware. Experiments were conducted on a $20^\circ \times 11.6^\circ$ (1920x1080 pixels), 32" Cambridge Research Systems Display++ with 120hz refresh rate. The Display++ was calibrated using a Photo Research PR 655 spectroradiometer with linearized gun outputs. To record their responses, participants used a handheld number pad. The experiments and color conversions were coded and presented using MATLAB 2022b and Psychtoolbox (Brainard, 1997).

Stimuli. The stimuli used for the visual search task had chromaticities defined within a scaled version of MacLeod-Boynton (MB) (D. I. A. MacLeod & R. M. Boynton, 1979) and Derrington-Krauskopf-Lennie (DKL) color spaces (Derrington et al., 1984b) (Figure 1). These spaces represent signals in terms of the cone-opponent axes (LvsM and SvsLM) at a constant luminance. The coordinates for the stimuli were defined by the following equations:

$$LvsM = (l_{mb} - 0.6568) * 1955, \text{ and}$$

$$SvsLM = (s_{mb} - 0.01825) * 5532$$

“ l_{mb} ” and “ s_{mb} ” are coordinates in Macleod-Boynton space and the values ‘0.6568’ and ‘0.01825’ are coordinates for the neutral grey with a chromaticity equivalent to Illuminant C. The values of 1955 and 5532 scale the values so that a 1-unit step along either axis corresponds very roughly to the threshold for detecting a color change from the white point (though thresholds were not measured for the current conditions). Thus, units along each axis correspond approximately to multiples of thresholds. In the results below, we also refer to these DKL coordinates by their polar angle, where “hue angle” refers to the direction from the neutral origin, and “contrast” refers to the distance from the origin.

Following McDermott et al., 2010, backgrounds corresponded to a dense array of overlapping ellipses, similar to “foliage,” formed by drawing 10,000 ellipses at random locations to fully pave all locations on the screen. Examples are shown in Figure 1. The size of each ellipse varied randomly in visual angle from 0.2° - 0.38° (minor axis) and 0.62° - 0.8° (major axis) and was also randomly varied in orientation. For backgrounds defined by a single chromatic axis, all ellipses had fell along the same axis but randomly varied in contrast over a range from ± 80 units in steps of 1 (for a total of 161 possible contrast values). Four different background axes were tested corresponding to angles of 150° - 330° (warm-cool), 120° - 300° (blue-yellow) and their respective orthogonal directions (60° - 240° and 30° - 210°) (Figure 2). For the multi-hued backgrounds, hue angle was instead randomly varied (from 0° to 360° sampled at 2.25° intervals) while the contrast was fixed at 20 (Figure 3). All backgrounds had a mean luminance of 20 cd/m^2 (equal to the target luminance), but the luminance of individual ellipses was varied over a range of $\pm 30\%$ of the mean to prevent luminance from being used as a cue to the target (Mollon, 1989b). Luminance was defined photometrically.

On each trial a single circular target stimulus was superimposed on the background. The target had a diameter of 0.5° and was displayed at a random position to the left or right side of the screen, excluding a horizontal region of 2° along the vertical midline. The chromaticities for the target angle varied along 12 different axes along the color space with 3 contrast levels (20, 40, or 80) at each angle, and had a fixed luminance of 20 cd/m^2 . Thus, in total we tested 36 different target colors on each of the backgrounds. The target axes included the 4 different background axes and were the same for all backgrounds.

For analyzing the search times, we assessed reaction times as a function of the difference of the target color from the background axis (C_d):

$$C_d = C_t \sin(\theta_t - \theta_b)$$

Where C_t is the absolute target contrast (relative to the white point), and θ_t and θ_b are the hue angles of the target and background (again each relative to the white point). A target that falls on the background axis thus has a contrast relative to the background of 0, while targets at angles perpendicular to the background have a relative contrast of C_t .

Procedure. Participants viewed the display binocularly in a darkened environment and sat 2 m from the screen. Each trial was signaled by a warning beep and then after a variable delay the target was displayed on the background and remained until the observer responded whether the target was on the left or right side, at which point the reaction time was recorded. During a single session, observers searched for all target chromaticities on each of two backgrounds (warm-cool versus orthogonal or blue-yellow versus orthogonal) which were presented in counterbalanced blocks of two sets each. Each target chromaticity was shown in random order on each background 10 times. Reported reaction times for individual observers are based on the median of the correctly responded repeated settings. Reaction times pooled across observers were based on the mean of the individual median values.

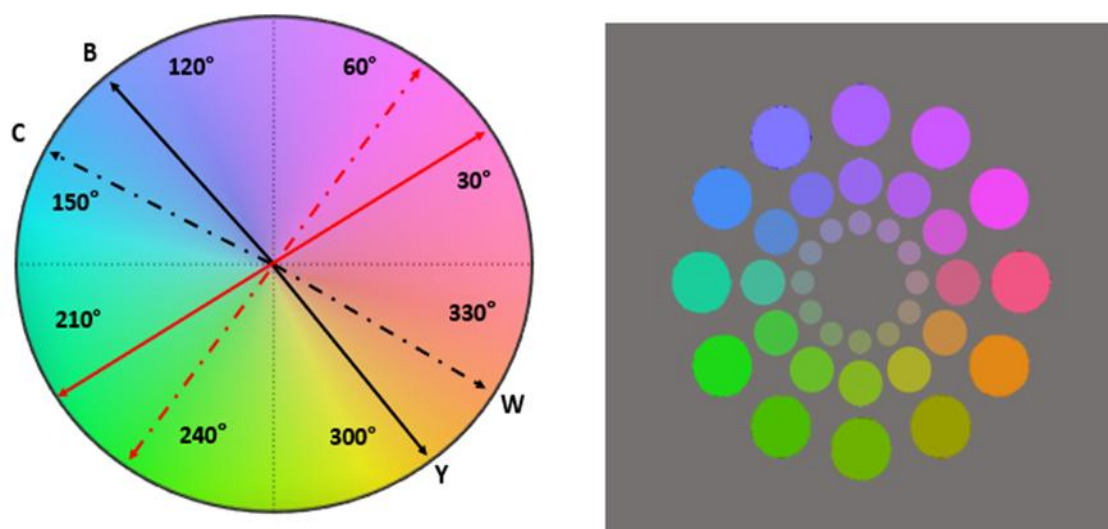


Figure 1. Left: the cone-opponent space showing the angles corresponding to the warm-cool axis (WC), the blue-yellow axis (BY) and the axis that is orthogonal to the WC (red-dashed line) or BY axis (red solid line). right: Chromaticities of the target colors, which spanned 12 chromatic axes including the 4 background axes and varied over 3 contrast levels (20, 40, or 80).

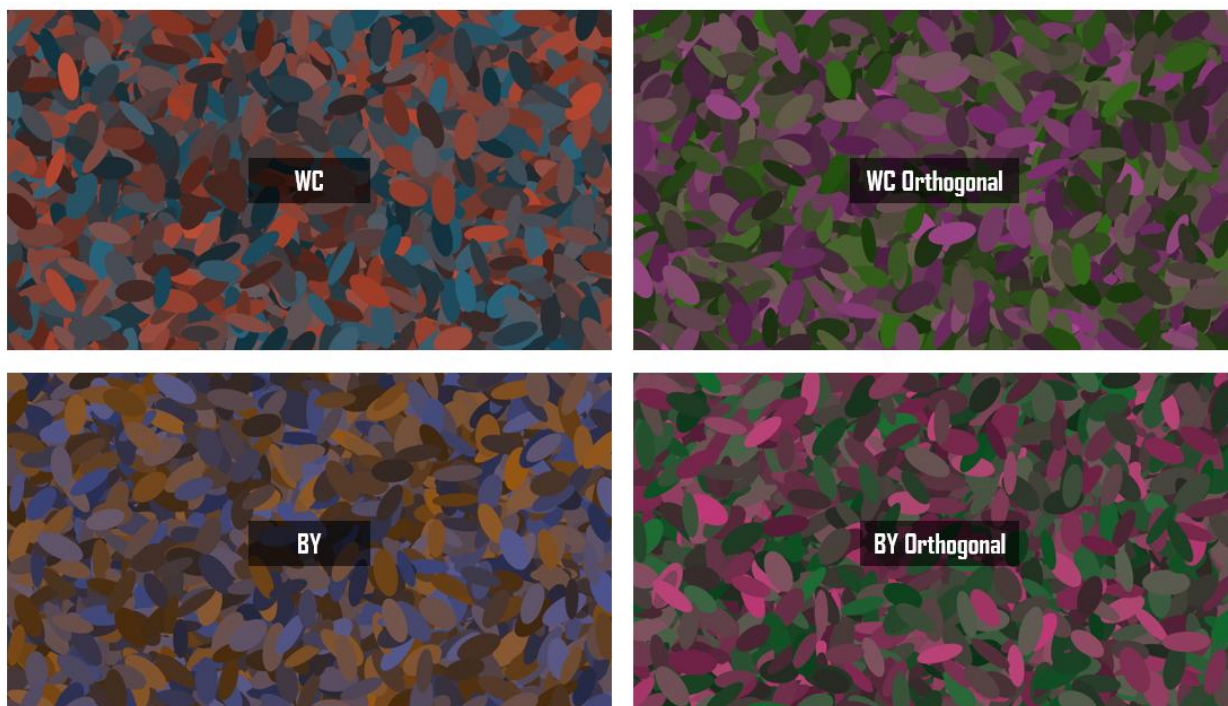


Figure 2. Backgrounds for the search task defined by variations along the warm-cool axis (WC), the blue-yellow axis (BY), the WC orthogonal axis, and BY orthogonal axis. Each background

corresponded to a fixed axis or hue angle in the color plane (as shown in figure 1) with contrasts of the elements randomly sampled over a range from -80 to $+80$ units.



Figure 3. Example of the uniform hue backgrounds. All chromaticities had a constant contrast of 20 relative to the achromatic point, and thus varied only in hue angle.

Results

Search for targets on Warm/Cool, Blue-Yellow, or Orthogonal backgrounds. Figure 4 illustrates the mean reaction times across observers on each of the 4 background axes. The two plots show results for targets shown on the warm-cool (Figure 4a) or blue-yellow (figure 4b) backgrounds, compared to the search times on the two corresponding orthogonal backgrounds. The relative contrast of each target chromaticity again varies with the background, and corresponds to the distance of the target chromaticity from the background axis (see eq 2). Thus, for each background, targets that lay along the background direction have an effective contrast of zero, while target colors perpendicular to the background axis have the highest contrast (up to ± 80). As expected and consistent with the results of McDermott et al. [19], search times fall consistently as the target-background distance increases. For small distances or zero contrast, color is not a cue

and they are limited by serial search for the target shape, while for high contrasts the targets effectively pop out.

However, Figure 4 also suggests that search times tended to be faster for the equivalent chromatic differences when the targets were shown on the warm-cool or blue-yellow backgrounds compared to the orthogonal backgrounds. To illustrate this more directly, Figure 5 shows scatterplots comparing the search times for equivalent target distances on each background, with the different colored symbols now showing the results for different individual subjects. Overall search times were substantially faster when the target colors were shown on the warm-cool background versus the orthogonal direction. A similar, though weaker, trend is also seen for the blue-yellow background, confirming the previous asymmetry found by McDermott et al. [19]. The magnitude of the differences in the reaction times are large, but may parallel the large color biases observed in natural color gamuts (Webster & Mollon, 1997) and in the sensitivity biases implicit in uniform color spaces (K. C. McDermott & M. A. Webster, 2012). The differences were assessed with sign tests comparing how often the reaction time for the equivalent target on one background exceeded the other. For this, the targets along each background (zero contrast) were excluded since no difference is expected for these stimuli. This showed significant differences in the search times for both the warm-cool and blue-yellow axes ($p < 0.0001$). We also compared the search times on the warm-cool vs the blue-yellow axes or between the two orthogonal axes. Scatter plots for these are shown on the two middle panels of Figure 5. However, despite the stronger asymmetries between the warm-cool or blue-yellow and orthogonal axes, the differences between the warm-cool and blue-yellow axes, approached but

did not reach significance ($p = 0.07$).

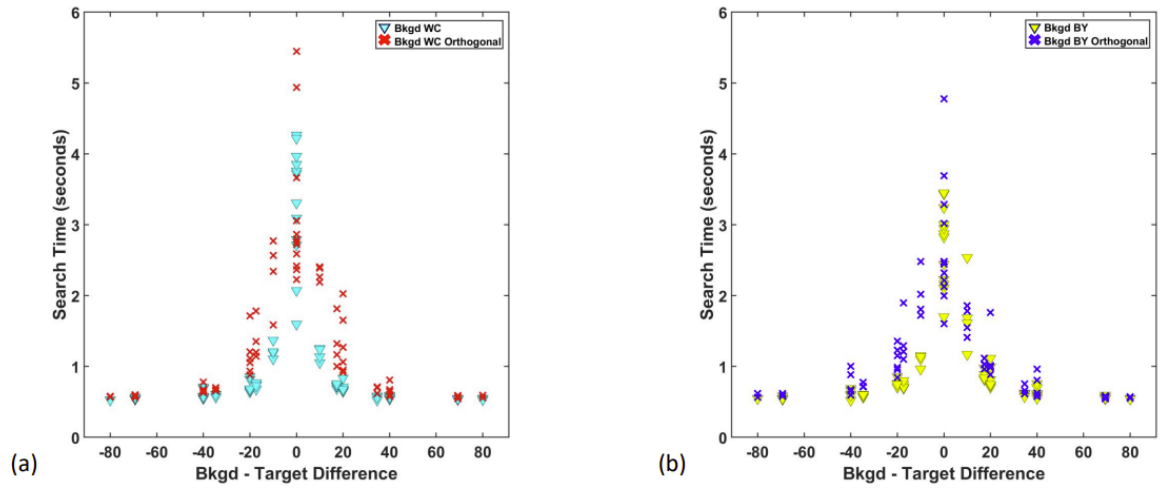
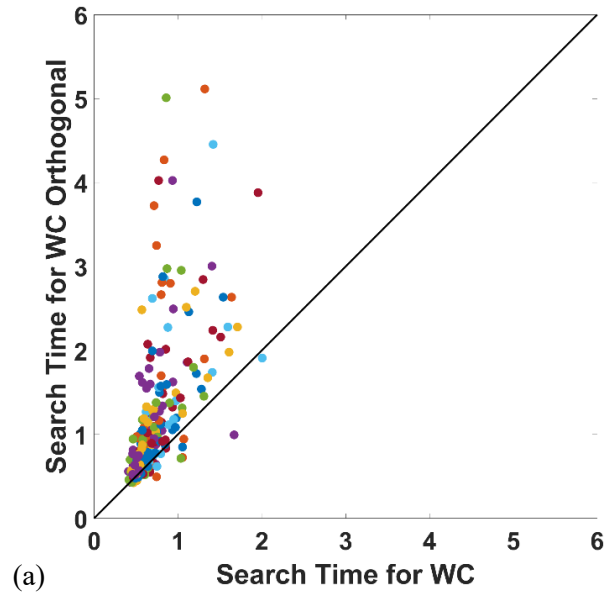
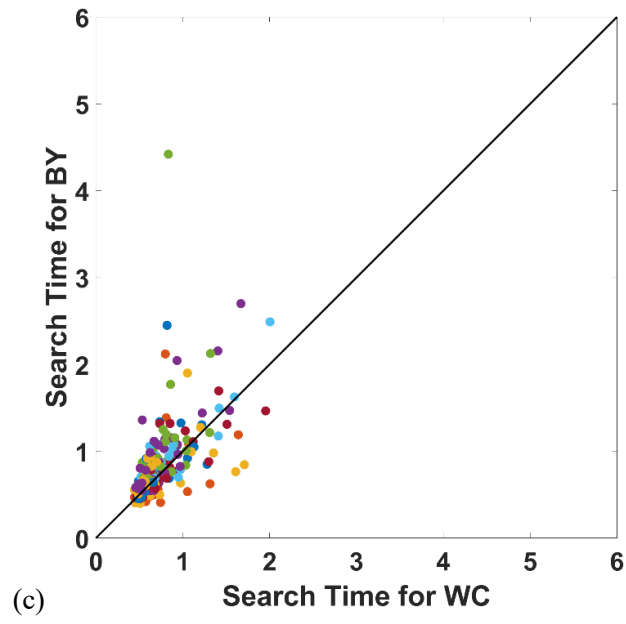
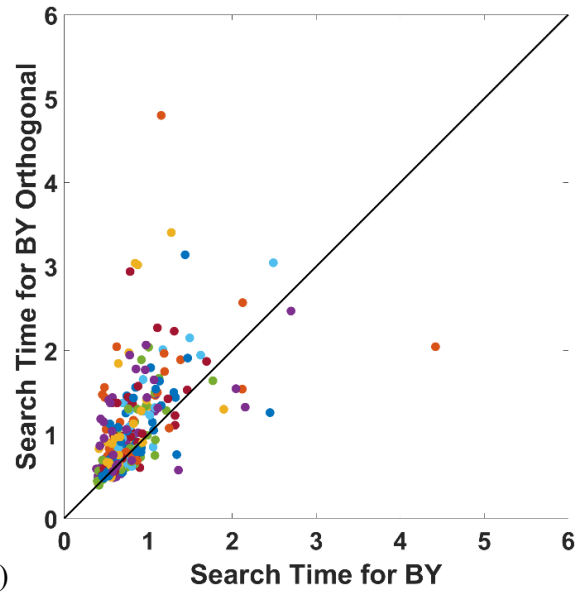


Figure 4. Search times (reaction time in seconds) plotted as a function of the colorimetric difference between the target and background axis. Each point corresponds to the average value of the individual observers' median reaction times for a given target, plotted as a function of the distance of the target from the background axis (as in eq. 2). (a) Blue triangles correspond to the warm-cool dimension and the red x's correspond to its orthogonal direction. (b) Yellow triangles correspond to the blue-yellow dimension and blue x's correspond to blue-yellow's orthogonal direction.





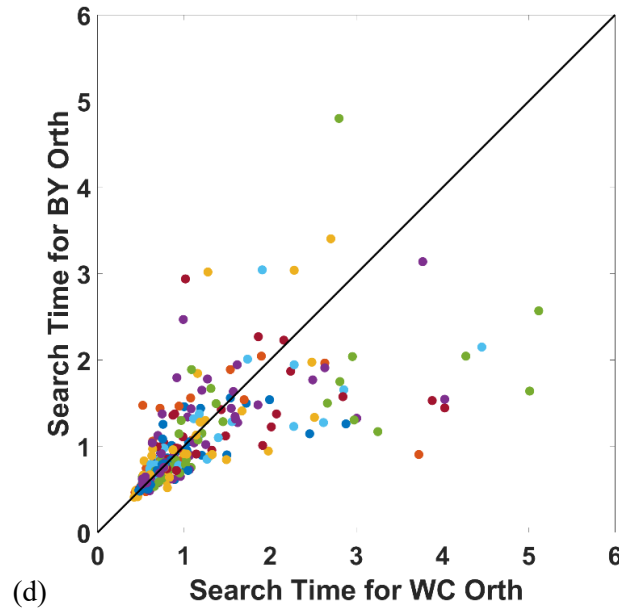


Figure 5. Top panels: Comparison of median search times (reaction time in seconds) for targets on the warm-cool background compared to targets on the orthogonal background (a), or for the blue-yellow versus the orthogonal background (b). Bottom panels: search times on the warm-cool versus blue-yellow backgrounds (c) or the two orthogonal backgrounds (d). Each point represents the median search time for a single observer and given target distance from the respective background.

Searching for warm targets versus cool targets or for blue targets versus yellow targets. As noted in the Introduction, a second goal of our study was to assess whether warm (or yellow) targets might be more salient and thus faster to find than cool (or blue) targets. In the first case, we examined this by comparing search times for targets with the same target background distance but in either the warm or cool direction, or blue or yellow direction, when measured on the orthogonal backgrounds. These comparisons are shown in Figure 6. For both cases, there are no clear advantages for the warmer or yellower hues, and this was confirmed by sign tests (warm versus cool $p = 0.07$; blue versus yellow $p = 0.55$).

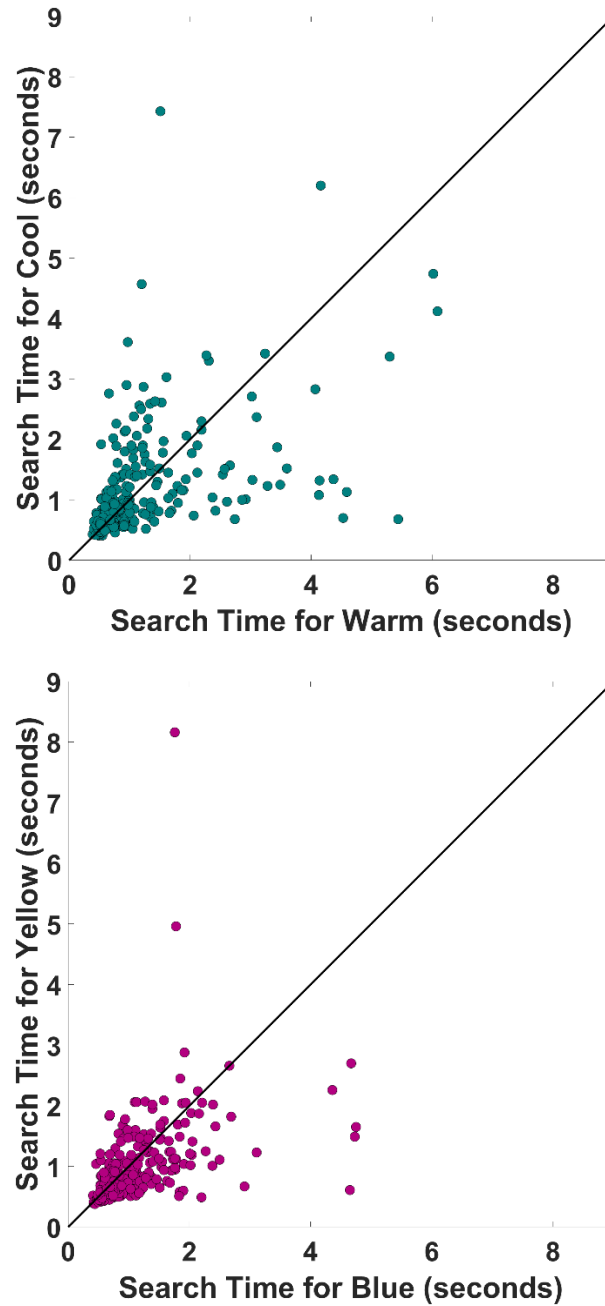


Figure 6. Comparison of median search times (reaction time in seconds) for warmer targets versus cooler targets (left) or yellower targets versus bluer targets (right) for individual observers.

The second way we explored this was with the multi-hued background illustrated in Figure 3, again with the same set of target stimuli. Average search times for 6 observers are shown in Figure 7. (Note the three contours correspond to RTs for absolute target contrasts of 20

(red), 40 (blue) or 80 (green), which correspond to differences of 0, 20, or 60 from the contrast of the background elements, which was 20.) Search times decreased as the target contrast exceeded the contrast of the background. However, there was not a consistent trend across the contrast levels for some hue angles to lead to faster detection. This was confirmed with a Kruskal-Wallis test of the reaction time differences across the 12 target angles, assessed separately for the three different target contrast levels. Differences were not significant at the 20 ($p = 0.76$) and 80 ($p = .078$) contrast levels, but were for the targets at a contrast of 40 ($p = .0014$). However, this difference is aligned along the LvsM vs SvsLM axes rather than the warm versus cool or blue versus yellow directions.

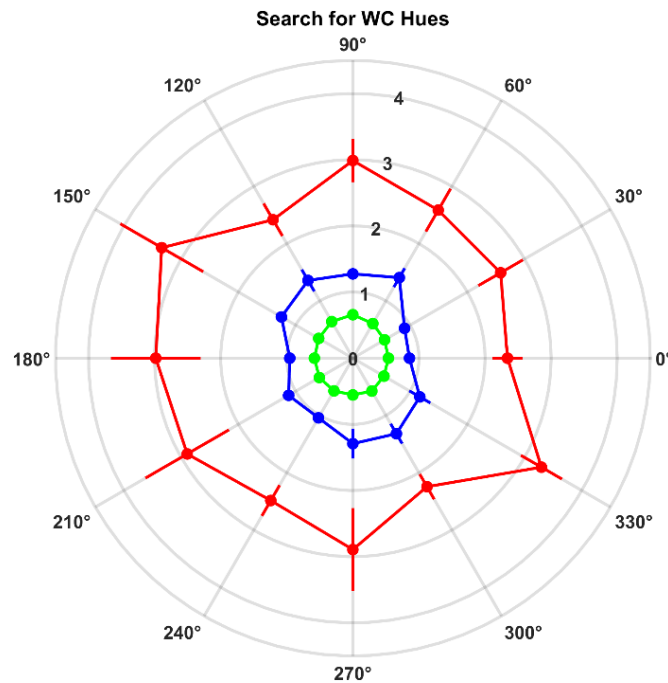


Figure 7. Polar plot showing average of the median search times (in seconds) for targets at different hue angles. Error bars correspond to ± 1 sd. Absolute targets contrasts were 20 (red), 40 (blue) or 80 (green), corresponding to color differences of 0, 20, or 60 units from the background contrast of 20.

Discussion

Many previous studies have demonstrated a sensitivity loss along the noncardinal bluish-yellowish direction of the cardinal cone-opponent plane (Webster & Mollon, 1997; Rudderman et al., 1998; Boynton et al., 1986; Bosten et al., 2015; McDermott et al., 2010; Juricevic et al., 2010; MacLeod & Boynton, 1979) and have generally attributed this to a blue-yellow bias in color vision. However, as we noted, uniform color space instead predicts a bias along more orange-cyan directions (McDermott & Webster, 2012), and we found that this corresponded closely to the axis defining the warm-cool dimension (Manalansan & Webster, 2023). Here our aim was to further test this correspondence by empirically measuring the relative salience of signals along warm-cool or blue-yellow axes as well as the orthogonal directions. Our results confirm previous findings from a similar color search task that targets that differed from a blue-yellow background were found more quickly than when the same target differences were shown on the orthogonal color background (McDermott et al., 2010). However, we also observed a similar and potentially stronger difference for the warm-cool background (Figure 5), though the differences for the warm-cool and blue-yellow background did not reach significance. The results therefore confirm that salience biases are again strong for the warm-cool axis, but may reflect a general sensitivity bias within the bluish-yellowish quadrants of the cone-opponent space.

Our second goal was to test for differences in the salience between different poles of the warm versus cool and blue versus yellow dimensions. Warm hues have been found to be disproportionately associated with objects while cool with backgrounds (Rosenthal et al., 2021), while yellow hues are more likely to be perceived as a surface color while blues an illuminant color (Pennock et al., 2023). This led us to hypothesize that warm and yellow hues might have more ecological salience than their cool and blue complements, potentially leading to a search

advantage. However, our results did not confirm this hypothesis, and instead show that for the conditions we examined there was little evidence for an asymmetry within either axis.

Notably, even though the warm-cool dimension is considered one of the most prominent attributes of color experience – our results confirm that the dimension is in fact composed of hues that have among the weakest perceptual salience. It remains to be determined why this is. One possibility is that while the color statistics of natural scenes have a characteristic blue-yellow bias (McDermott & Webster, 2012; Webster & Mollon, 1997; Skelton et al., 2024), few people live in natural outdoor environments, and constructed environments may include a greater proportion of warm hues. Given their association with objects (Rosenthal et al., 2021), we may also spend more time looking at warm colors. Both of these effects could lead to a disproportionate exposure to warmer hues, which could in turn lead to stronger adaptation and reduced sensitivity to this dimension. Further studies are needed to explore the color statistics of modern human environments and how observers visually sample them, as well as to explore other perceptual correlates of the warm-cool division of color.

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Chapter 4. Saliency of warm-cool and blue-yellow

Abstract

Adaptation and color perception are shaped by environmental factors, such as the colors found in the different types of environments, we find ourselves in. The warm-cool and blue-yellow dimensions have been proposed as fundamental perceptual axes which reflect how chromatic statistics tune the visual system. In this study, we investigated whether these axes differ in their perceptual saliency compared to their orthogonal magenta-green axes. Fifteen observers judged grid-like diamond patterns varying in contrast levels in a method of constant stimulus task. We used a perceptual grouping task where participants judged the orientation of grid-like diamond patterns to measure the relative contrast sensitivity of different chromatic axes. Stimuli were defined in a scaled version of cone-opponent space comparing warm-cool and blue-yellow conditions against their orthogonal (magenta-greenish) references at three contrast levels. Both warm-cool and blue-yellow required higher contrast than their orthogonal counterparts to achieve perceptual equivalence indicating systematic biases in contrast, where both WC and BY stimuli required higher physical contrast than their orthogonal counterparts to achieve perceptual equivalence. Importantly, the two conditions showed distinct patterns: a repeated measures ANOVA showed warm-cool bias increased with each reference contrast step increase, while blue-yellow showed a non-linear relationship with the increase in reference contrast. These findings demonstrate that warm-cool and blue-yellow axes are processed differently compared to magenta-greenish stimuli. The results support previous findings which show warm-cool and blue-yellow have lower perceptual saliency compared to their orthogonal directions.

Introduction

Certain perceptual judgements, specifically, warm-cool distinctions of color experience are still poorly understood and considered a fundamental aspect of color experience. Whether or not the warm-cool dimension reflects cortical representations which align with perceptual dimensions (Rosenthal et al., 2021), whether it is a learned association concerning specific modalities of the natural environment, such as learning to associate heat with red because of our interactions with flames (Ho et al., 2014), or whether it reflects a combination of these two ideas that perceptual spaces are neither innate nor entirely learned is still unclear (Koenderink & Van Doorn, 2021). The debate as to what constitutes warm vs cool judgements has recently gained further traction with studies pinpointing color direction that the warm-cool dimension lies around the orange-teal direction (Koenderink & Van Doorn, 2021; Manalansan & Webster, 2023).

Previous studies have attributed other modalities and features of the world to the warm-cool distinction. For instance, some have attributed this dimension to the object-background distinction; objects are considered warmer than the backgrounds those objects are in (Gibson et al., 2017; Pennock et al., 2023). Others have shown individual variation of these warm-cool judgements when measuring them with regards to lightness (Devinck & Knoblauch, 2024). The way our color perception is tuned by the environment may shape its characteristics and individual variations as well (Long et al., 2006; Long & Purves, 2003). The color statistics of the environment shapes how we encode and make judgements about color. What this means for the visual diet of the observers has also been assessed in a growing body of work claiming that the colors in the environment are much closer towards a bluish-yellowish hues; frequent exposure to certain chromatic distributions, e.g., those found in natural daylight, can bias perceptual color tuning (Skelton et al., 2024; Webster, 2020; Webster & Mollon, 1997). This bias in tuning may be the underlying cause of asymmetries in uniform color spaces such as CIELAB and CIELUV.

Uniform color spaces are designed so that equal distances represent equal perceptual distances, yet they show non-uniform scaling across different chromatic directions. The blue-yellow axis shows compressed perceptual scaling compared to other chromatic directions, while the warm-cool axis shows similar asymmetric patterns (Manalansan & Webster, 2023). These asymmetries may reflect adaptive tuning to environmental color statistics, where frequently encountered chromatic variations become perceptually compressed, requiring larger physical changes to achieve equivalent perceptual differences. This adaptive compression affects fundamental aspects of color perception, the stronger a stimulus is, the more the system must adapt to that stimulus, resulting in weaker sensitivity.

Judgements of warm versus cool have been shown to remain relatively stable between cultures and individuals (Ou et al., 2004, 2012). In a previous study, using a judgement task, we found large individual differences in the warm cool axis but these were stable across changes in lightness (Manalansan & Webster, 2023; McDermott & Webster, 2012). In a recent visual search study, we had shown how blue-yellow and warm-cool (orange-teal) backgrounds affected perceptual foraging tasks. Our results showed that targets embedded in blue-yellow or warm-cool backgrounds were located more readily than targets embedded in reddish-greenish contexts (Manalansan, Simoncelli, et al., 2025). This suggested that certain color axes may be perceptually "discounted". This may potentially be due to adaptive mechanisms which allow other colors to stand out more easily. Targets stood out from blue-yellow and warm-cool distractors because the visual system may be discounting the orangish-teal colors (and bluish-yellow colors). To further test this hypothesis, we examined whether WC and BY axes show reduced perceptual salience compared to their orthogonal directions.

Color plays a fundamental role in perceptual organization and visual grouping, enabling the visual system to segment scenes and organize visual information (Wolfe & Horowitz, 2017).

Different chromatic axes contribute differently to these organizational processes, with some color directions being more salient for perceptual grouping tasks than others.

To test whether WC and BY axes show reduced perceptual salience compared to their orthogonal directions, we employed a perceptual grouping task using grid-like diamond patterns in a method of constant stimuli. The study made use of stimuli similar in vein to a paradigm used by Regan and Mollon (Regan & Mollon, 1997). However, instead of comparing the salience of the S vs LM axes we instead compared the WC or BY axes to their orthogonal color directions in order to test and compare the relative strength of the two axes in perceptual grouping. We measured the point of subjective equality (PSE), i.e., the contrast level at which participants are equally likely to perceive the test chromatic direction versus its orthogonal counterpart. Higher PSE values indicate that the test direction requires more contrast to achieve perceptual equivalence with the orthogonal reference, suggesting lower perceptual salience for that chromatic axis.

We tested performance at three fixed contrast levels (10, 20, and 40) for the orthogonal reference direction to examine how the relative salience of WC and BY axes changes across the dynamic range of contrast processing. Testing across multiple contrast levels (low, medium, and high) is critical because this ensures robust results capturing as much information as possible. We hypothesize that if WC and BY axes are perceptually discounted due to adaptive mechanisms, they should require higher contrast than their orthogonal directions to achieve perceptual equivalence (PSE ratios > 1.0). We aimed to determine which axis—BY or WC—shows the least sensitivity. The BY axis corresponds to the axis of illumination variation in natural scenes, while the WC axis aligns with the direction of least sensitivity predicted by asymmetries in CIELAB color space. By testing across multiple contrast levels, we can determine both the sensitivities of both BY and WC and which axis shows least sensitivity.

Methods

Participants

Participants for the study included the author J.M. and 14 ($N = 15$) students recruited from the University of Nevada, Reno (UNR). For a follow up experiment to measure the effect of scaling with our color space, $N = 6$ of observers from the original study were asked back to participate in a separate experiment measuring cardinal axis scaling. One participant in the original study was excluded from analysis because of poor psychometric function fits (R^2 values decreased as contrast increased $0.695 \rightarrow 0.396 \rightarrow 0.011$) suggesting the outlier participant's performance became increasingly inconsistent at higher contrast levels. It could be that the outlier did not understand the task. Participation in, and procedures of, the study were conducted with informed consent following UNR's IRB protocols. The participants were tested for color normalcy using Ishihara Plate tests.

Apparatus and Hardware

Stimulus presentation and experimental procedures were conducted on a 32 in. Cambridge Research Systems Display++ monitor with a 120 Hz refresh rate and dimensions of $20^\circ \times 11.6^\circ$ (1920 x 1080 pixels). The monitor was calibrated using a Photo Research PR-655 spectroradiometer. When recording the responses for the study, participants used a handheld number pad. Experiments and color conversions were coded using MATLAB 2022b and Psychtoolbox (Brainard, 1997).

Stimuli and Paradigm

Chromaticities for the stimuli were defined within a scaled version of MacLeod-Boynton (MacLeod & Boynton, 1979) and Derrington-Krauskopf-Lennie (Derrington et al., 1984) color

spaces with cone-fundamentals based on the standard by Stockman and Sharpe (Stockman, 2019; Stockman & Sharpe, 2000). These two spaces represent signals of the cone-opponent axes (L vs M and S vs LM) at a constant luminance of 20 cd/m². Coordinates for the stimuli were defined through the following equations:

$$\text{L versus M} = 2500 * (I_{mb} - 0.6981),$$

$$\text{S versus LM} = 5000 * (S_{mb} - 0.02065),$$

the values 0.6981 and 0.02065 are the l and s coordinates of D65. The stimulus itself was a 10 x 10 array of 0.5° circles arranged in a grid-like diamond pattern in front of a grey background equiluminant at 20 cd/m². The stimulus array was centered on the background of the display and was shown for 1000 ms on followed by the grey screen with infinite response time to allow the participant to make a judgement (see Fig. 1).

Along cone-opponent space, color coordinates for the BY condition were set at 120° - 300°, corresponding to the unique blue-yellow axis, and its orthogonal direction at 30° - 210°. Coordinates for the WC condition was set at 150° - 330° along cone-opponent space, corresponding to the warm-cool (orangish-teal) axis (Manalansan, Whitehead, et al., 2025) with its orthogonal direction at 60° - 240°. In each trial, the orthogonal directions (magenta-green) were presented at a fixed contrast level while the test direction (WC or BY) was varied in contrast per fixed contrast condition in steps of 9 units. We used three fixed contrast levels (10, 20, 40 units) to examine how the relative salience of these chromatic axes' changes across the dynamic range of contrast processing. For a fixed contrast at 10, contrast was varied for BY and WC from 0 to 20 units in steps of 2.5. For a fixed contrast at 20, contrast was varied from 5 to 45 units in steps of 5; and for fixed contrast at 40, contrast was varied from 16 to 80 units in steps of 8. This allowed us to sample an adequate proportion of responses for each fixed contrast

condition; meaning we systematically varied the test contrast around the expected PSE, i.e., a PSE of 1.0, to adequately sample around the psychometric function.

Control Experiment

Color space scaling was validated through a control experiment with six participants who completed an additional session testing the cardinal L vs M and S vs LM axes. This control revealed a scaling bias of leading to very minor correction of all experiment data by a factor of 0.9875 applied to the S vs LM component.

Procedure

Before the testing procedure could begin, participants were tested in a separate room for color normalcy using Ishihara Plate tests and excluded from study if they fail color vision assessment. In the constant stimulus task, the participant was shown the stimulus in randomized order with each of the nine-contrast stimulus for the each of the three randomized fixed contrast conditions tested at 10 repetitions for WC and BY each. BY and WC conditions were tested within the same experimental session in intermixed trials. Participants viewed the display binocularly in a darkened room from a distance of 200 cm. A total of 1080 trials was tested for each participant. Each test stimulus was presented with a random color condition (BY or WC) and a random varied and fixed contrast condition. The participant judged whether the test stimulus was either pointing towards the leftward diagonal or the rightward diagonal.

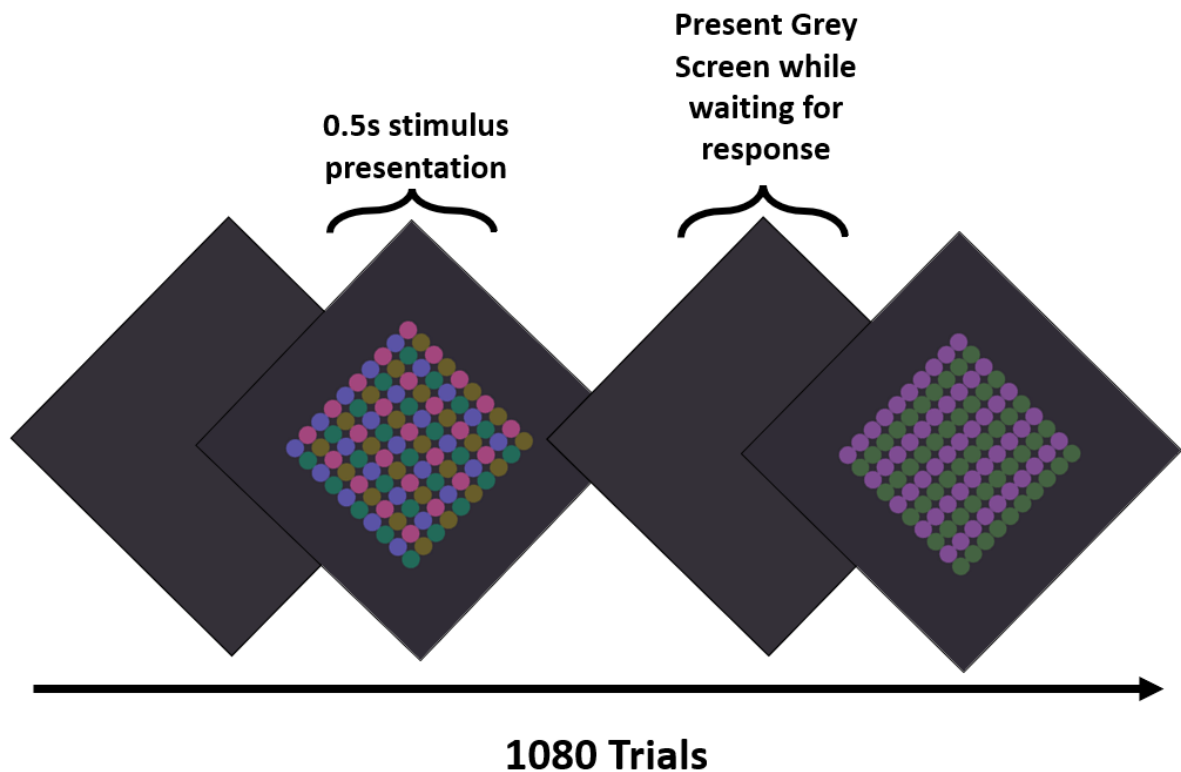


Figure 1. Experimental procedure of 10x10 grid-like pattern. A 0.5s presentation followed by a grey screen. Next stimulus was not presented until the participant had decided as to whether they view the test stimulus either pointing towards the left or the right diagonal.

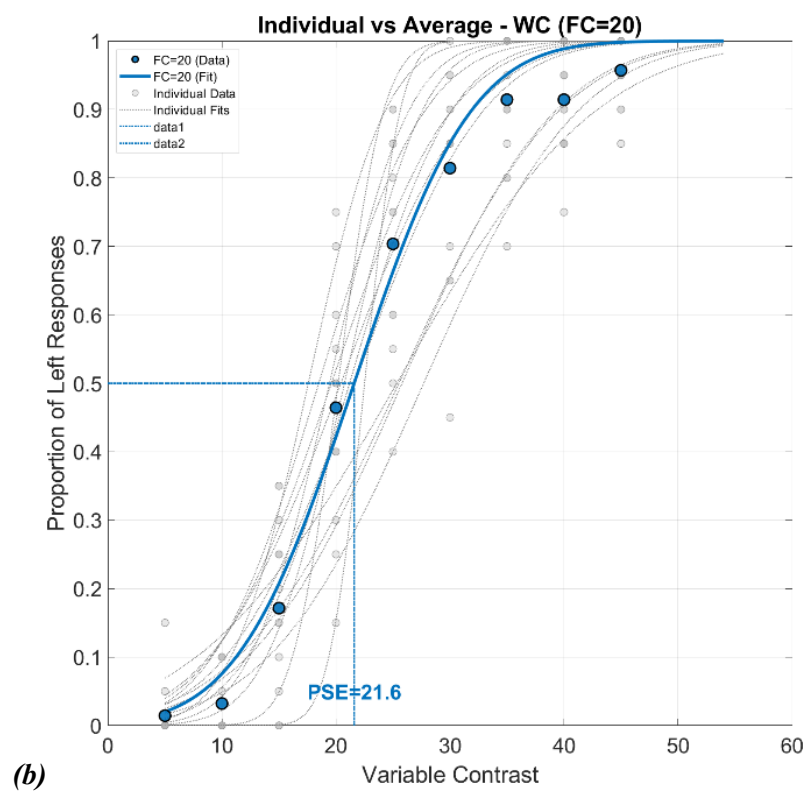
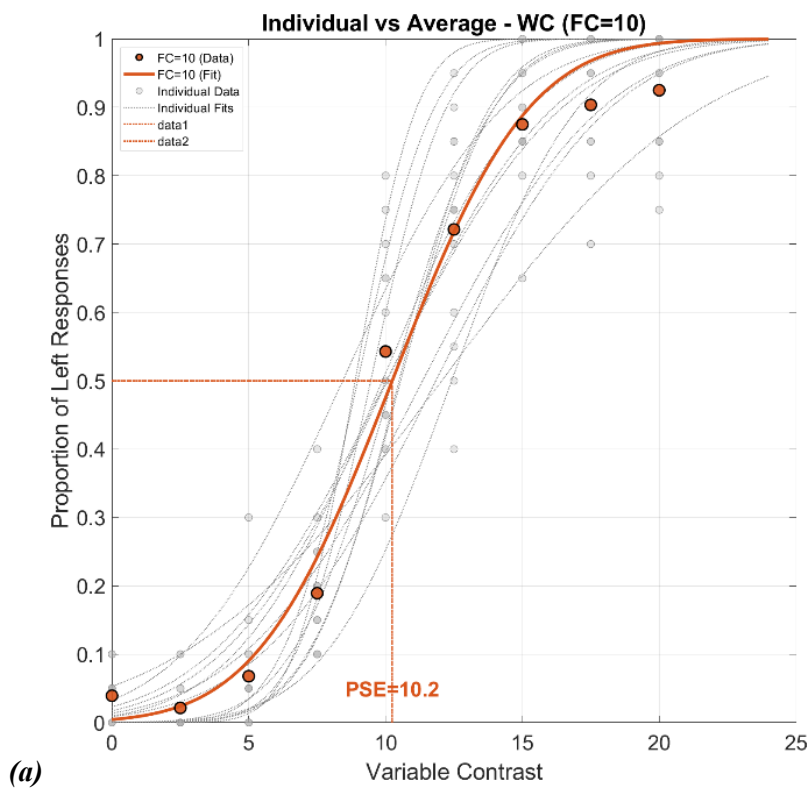
Results

PSE and Psychometric Functions. Psychometric functions relating the variable contrast to the proportion of left responses, i.e., how often the participants saw the stimuli pointing at a leftward diagonal, yielded consistent curves across both warm-cool (WC) and blue-yellow (BY) conditions. Cumulative Gaussian functions were fitted to individual and aggregated data with R^2 values consistently exceeding 0.85 across conditions and contrast levels. The fits from these psychometric functions enabled reliable extraction of point of subjective equality values, which represent the contrast level at which participants perceived the test and reference stimuli as equal

in perceptual strength. These PSE values were subsequently corrected for chromatic scaling effects brought on by the scaled color space we used on our stimuli, i.e., the bias in the relative scaling of the L vs M and S vs LM axes, to yield normalized PSE ratios which were used in our statistical analysis.

Figures 2-3 illustrate the representative psychometric functions showing the relationship between variable contrast and the proportion of responses for both individual participants (grey dotted lines) and group averages (colored solid lines). Vertical dotted colored lines indicate the PSE -- the contrast value at which participants perceived equal strength between the variable and fixed contrast (or the point at which the stimuli can be perceived either pointing upward toward the leftward diagonal or towards the rightward diagonal). In analyzing the functions and PSEs, several notable patterns emerged which reveal fundamental differences in contrast processing between WC and BY.

For the WC condition, the psychometric functions exhibited a systematic positive trend as fixed contrast (FC) increased from 10, 20, to 40, PSE values also increased. At FC = 10, group mean PSE occurs at ~10.2 variable contrast (VC) showing minimal increase in contrast gain to achieve perceptual equivalence (Figure 2a). As the FC increases, the bias becomes progressively more pronounced. PSE value at FC = 20 occur at ~21.6 and PSE value for FC = 40 occur at 46.5 VC (see Figure 2a-c). This pattern suggests that the WC pathway exhibits contrast-dependent changes in perceptual bias; the magnitude of bias increases systematically as the fixed contrast level also increases. This could reflect adaptive mechanisms where higher contrast stimuli require progressively greater variable contrasts to achieve subjective equality and might be consistent with studies showing gain control effects in chromatic vision (Solomon & Lennie, 2005).



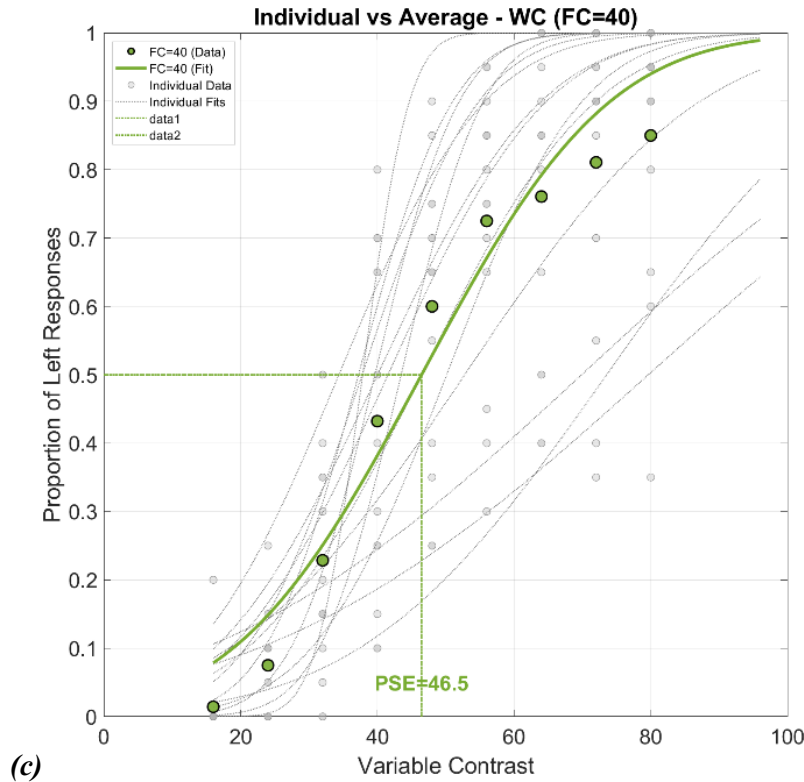
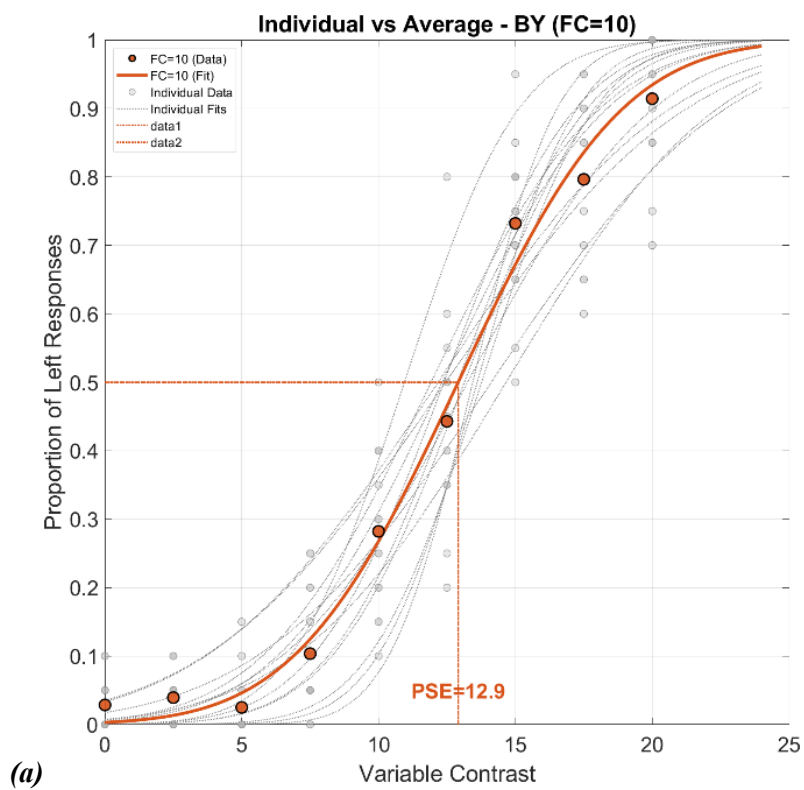


Figure 2. Individual (grey) vs Average (colored) PSE and psychometric functions for the WC condition. (a) PSE for FC = 10 shows minimal bias with a ratio ≈ 1.02 . (b) PSE for FC = 20 shows increased bias with a ratio ≈ 1.09 and (c) PSE for FC = 40 shows substantial increased bias with PSE ratio ≈ 1.21 .

The BY condition presents a different trend to the WC condition. Across all contrast levels, the psychometric functions are consistently shifted rightward compared to their WC counterparts, indicating stronger biases with the BY condition (see Figure 3a-c). The magnitude of the rightward shift remains relatively stable across fixed contrast levels. PSE value at FC = 10 occurs at ~ 12.9 ; PSE value at FC = 20 occurs at ~ 24.8 ; and, PSE value at FC = 40 occurs at ~ 50.7 . While absolute PSE values increased with fixed contrast, the PSE ratios remain relatively stable ($1.293 \rightarrow 1.242 \rightarrow 1.276$). This contrasts with the systematic increase observed in the WC condition. Both the WC and BY axes show reduced perceptual salience compared to their orthogonal directions, with the BY axis showing weaker sensitivity overall. The BY axis

maintains substantial bias across all contrast levels tested, while the WC axis shows a more gradual increase with contrast.



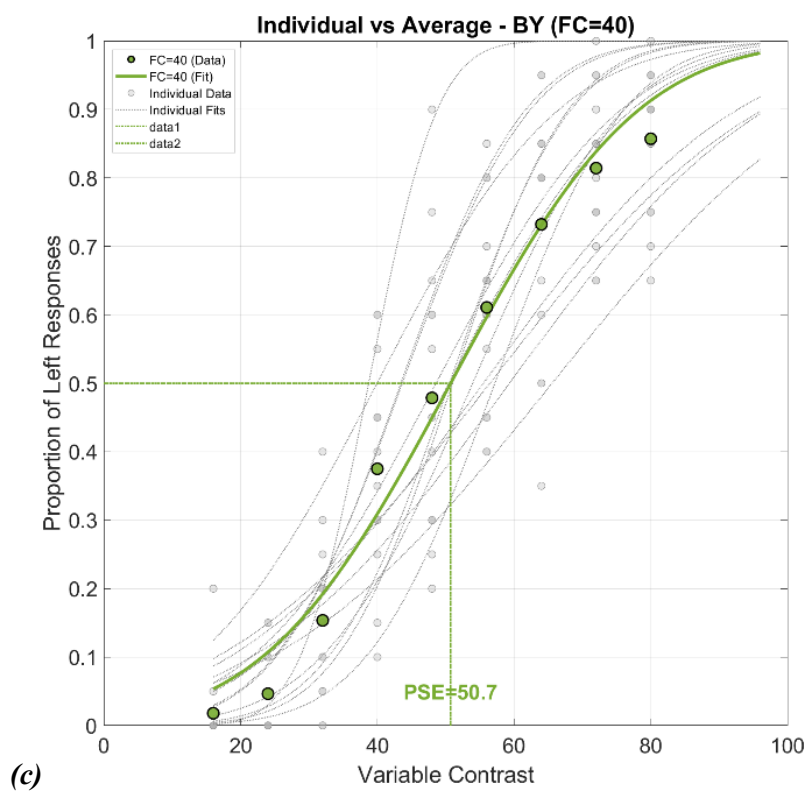
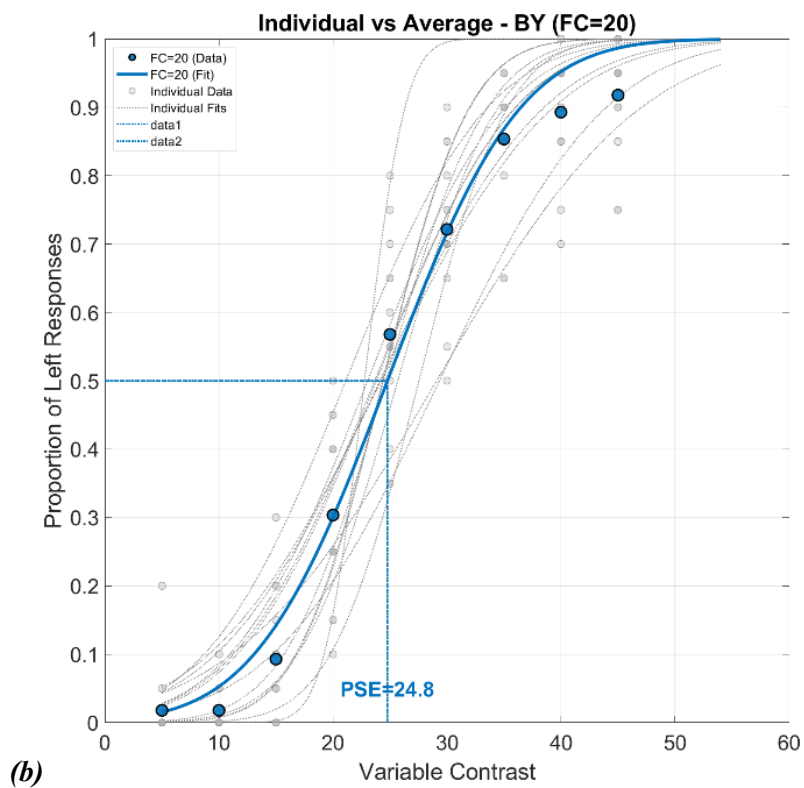


Figure 3. Individual vs Average PSE values and psychometric functions for the BY condition. Much like the WC condition, the BY condition shows increase PSE value compared to the fixed contrast condition in order to achieve perceptual equivalence. (a) PSE value at FC = 10 occurs at ~12.9. (b) PSE value at FC = 20 occurs at ~24.8. (c) PSE value at FC = 40 occurs at ~50.7.

Individual participant data (shown in grey dots) reveal substantial individual differences and variability. For both WC and BY, these individual differences are more pronounced at the highest contrast level (FC = 40). Individual psychometric functions show that while the general pattern of pathway differences holds across participants, the magnitude of these differences varies substantially between individuals. Some participants show steeper sigmoidal curves than others, and the spread of the individual data points around the fits increases systematically with contrast increases. This suggests that individual differences in contrast processing becomes more apparent under conditions of higher chromatic stimulation. Anecdotally, some participants reported increased after-image effects at higher contrast levels as well.

Accounting for Color Space Bias. Our main experiment used a scaled version of cone-opponent space which may have introduced systematic biases in the relative scaling of the L vs M and S vs LM axes. To test for this potential artifact, we conducted a control experiment to understand the extent this bias may have influenced our analyses. Incorrect scaling of the color space would systematically bias our PSE measurements. If the S vs LM axis is compressed or stretched relative to L vs M, this would artificially inflate PSE ratios for any direction containing an S vs LM component, including both BY and WC conditions.

Methods. Six participants from the original study completed an additional experiment measuring PSE values for the cardinal L vs M and S vs LM axes using identical procedures to the main experiment. The cardinal axes were tested at the same three fixed contrast levels (10, 20, 40) with the same method of constant stimuli paradigm.

Results. The control experiment revealed deviations from unity or deviations from 1.0 in our original color space scaling. Mean PSE ratios across all cardinal axis conditions were (Table 1):

Table 1. Control experiment results: L vs M and S vs LM axes for 6 participants.

Fixed Contrast	Mean PSE Value	Mean PSE Ratio	SE
10	9.86	0.989	0.061
20	19.12	0.961	0.034
40	39.81	1.013	0.062
Overall	22.93	0.988	0.029

The mean PSE ratio across all cardinal axis conditions was 0.9875, indicating that our original color space scaling systematically underestimated contrast requirements by approximately 1.25%. This deviation from a PSE ratio = 1.0 suggested that our color space required correction. The mean deviation of only 1.25% from unity confirms our original scaling was largely accurate. Nevertheless, we applied this small correction to ensure complete accuracy in our results. Individual participants showed varying degrees of bias in the cardinal axis measurements, with PSE ratios ranging from 0.805 to 1.235 across participants and contrast levels. However, the systematic deviation from unity was consistent across the group (falling below 1.0).

Correction Procedure. All main experiment PSE values were corrected by applying a scaling factor of 1.0126 (calculated as $1/0.9875$) to normalize the cardinal axes to unity. This correction was applied by multiplying the S vs LM component of all chromatic coordinates by 0.9875. After correction, the cardinal axes yielded mean PSE ratios of approximately 1.0, validating that differences between WC/BY and their orthogonal directions in the main experiment reflect genuine perceptual asymmetries rather than color space artifacts. Figure 4 shows the extent of the color space bias. This correction slightly rotates both the BY and WC axes in color space, bringing them closer to their intended positions. The effect is minimal but ensures our test directions accurately represent the WC and BY axes. The overall mean PSE ratio (0.9875, SD =

0.088, SEM = 0.036) was not significantly different from 1.0 (one-sample t-test: $t(5) = -0.347$, $p = 0.743$), indicating that our color space scaling was essentially correct.

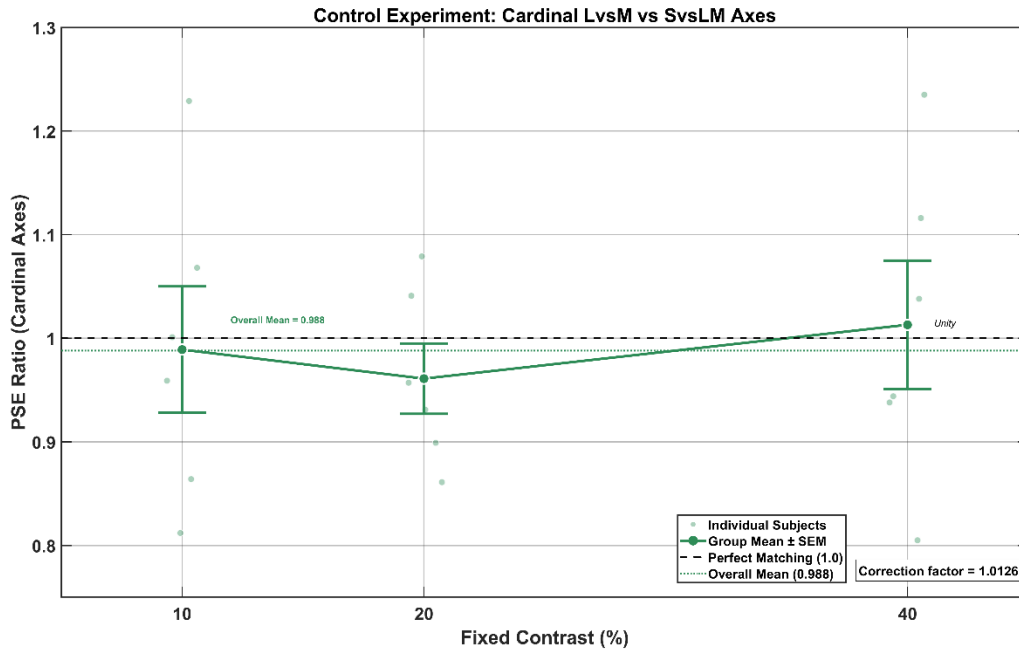


Figure 4. Average PSE ratios showing the effect of color space bias. Error bars represent ± 1 SEM ($n = 6$). Individual subject data shown as semi-transparent points. The dashed line represents perfect contrast matching. Mean PSE ratio of 0.9875 indicated systematic scaling bias in the original color space, leading to correction of 1.0126 applied to all main experiment data, however, the mean ratio was not significantly different from perfect scaling of 1.0 ($p = 0.743$).

The corrected PSE ratios provide a normalized measure of perceptual bias that accounts for relative contrast levels and color space scaling artifacts. Table 2 summarizes the mean PSE ratios and standard errors across all 14 participants:

Table 2. Mean corrected PSE ratios and standard errors by condition and fixed contrast level.

Fixed Contrast	WC Condition		BY Condition	
	Mean	SE	Mean	SE
10	1.027	0.031	1.302	0.025
20	1.087	0.039	1.250	0.030
40	1.215	0.095	1.284	0.050

Several key patterns emerge from these data. All PSE ratios exceeded 1.0 indicating a consistent perceptual bias across both WC and BY conditions. Observers required higher contrast to achieve subjective equality with the fixed contrast stimulus. However, the magnitude of the bias differs between WC and BY. For the BY condition, PSE ratios were consistently higher (ranging from 1.25 to 1.30) compared to the WC condition (ranging from 1.03 to 1.21) indicating fundamental differences in the characteristics of these two conditions. Figure 5 shows the two conditions demonstrate distinctly different patterns of contrast modulation. The WC condition shows a clear positive trend or positive relationship between fixed contrast level and PSE ratio. At low contrast (FC = 10), there is minimal bias at a ratio ≈ 1.03 and progressing to a substantial bias at high contrast (FC = 40) with a ratio ≈ 1.21 . The BY condition a more complicated, non-monotonic, relationship with contrast level. The PSE ratio is highest at the lowest contrast level (FC = 10, ratio ≈ 1.30), decreases at the middle contrast level (FC = 20, ratio ≈ 1.25), then increases again at the highest contrast level (FC = 40, ratio ≈ 1.28).

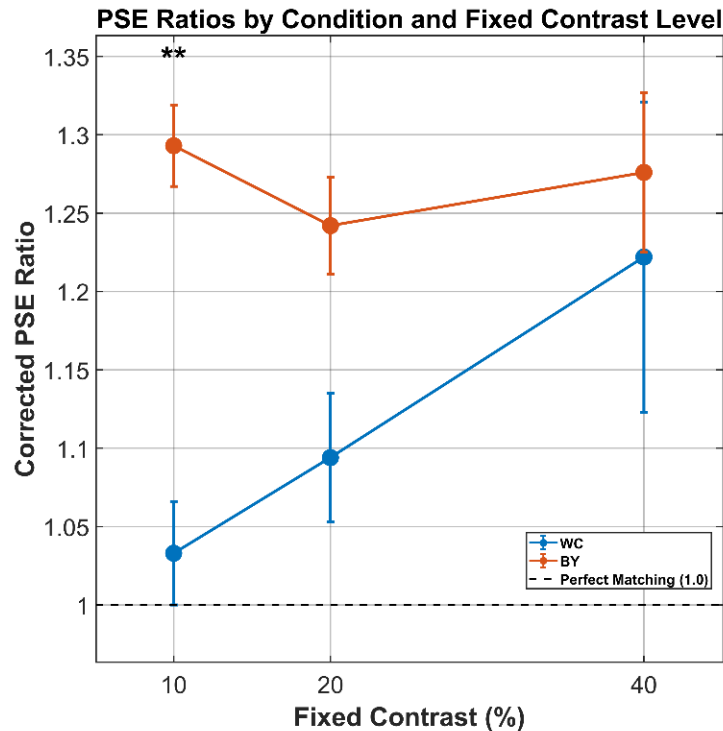


Figure 5. PSE ratios as a function of fixed contrast level for WC (blue points) and BY (orange points) conditions. Error bars represent ± 1 SEM. Double asterisks (**) indicate significant differences between conditions at that contrast level with Bonferroni correction ($p < 0.017$). The dashed horizontal line across the x-axis represents perfect contrast matching (no bias). Both conditions show PSE ratios consistently above 1.0, indicating systematic bias, with BY showing significantly higher ratios than WC at low contrast levels.

Statistical analysis of group and simple effects. Using the corrected PSE proportions a 2x3 repeated measures ANOVA was conducted with the two conditions (WC & BY) and fixed contrast level (10, 20, & 40) as within subject factors. Mauchly's test indicated that sphericity assumptions were met for all effects (all $p > 0.05$). The analysis revealed a significant main effect of condition, $F(1, 13) = 7.35$, $p = 0.018$, $\eta^2 = 0.361$, confirming the PSE ratios differing systematically between the WC and BY conditions). The main effect of fixed contrast level neared/approached (but did not achieve) significance, $F(2, 26) = 2.83$, $p = 0.078$, $\eta^2 = 0.179$. An interaction between condition and fixed contrast level also approached, but did not achieve,

significance, $F(2, 26) = 2.60$, $p = 0.094$, $\eta^2 = 0.167$. However, interaction effects were observed with the condition vs subject analysis, $F(13, 26) = 2.87$, $p = 0.011$, $\eta^2 = 0.584$, indicating substantial individual differences in the relative magnitude of WC and BY biases.

One-sample t-tests determined whether PSE ratios differed significantly from 1.0 (indicating bias away from perfect contrast matching). For the WC condition, FC10 did not reach significance: $t(13) = 1.03$, $p = 0.335$; FC20 did reach significance: $t(13) = 2.29$, $p = 0.039$; and FC40 also reaching significance: $t(13) = 2.24$, $p = 0.043$. For the BY condition, all three fixed contrast levels reached highly significant results. FC10: $t(13) = 11.3$, $p < 0.001$; FC20: $t(13) = 7.8$, $p < 0.001$; and FC40: $t(13) = 5.4$, $p < 0.001$. These results confirm that both axes show systematic biases (reduced perceptual salience) compared to their orthogonal directions, with BY showing stronger bias overall.

Given the interaction between condition and fixed contrast did not achieve significance, simple effects analyses examined contrast-dependent changes within each condition separately. The simple effects analyses revealed a significant effect of fixed contrast level was observed for the WC condition, $F(2, 26) = 4.19$, $p = 0.026$, $\eta^2 = 0.244$. A post-hoc Bonferroni correction revealed a significant difference between the fixed contrast levels 10 and 40 ($p = 0.031$) confirming the contrast dependent changes in perceptual bias for the WC condition. Comparatively, the BY condition showed no significant effect of fixed contrast level, $F(2, 26) = 1.28$, $p = 0.295$, $\eta^2 = 0.09$, confirming that there was no systematic linear trend in PSE ratios across contrast levels.

Discussion

The present study investigated perceptual biases along warm-cool (orange-teal) and along blue-yellow (unique hue) color axes and how these biases vary with contrast along a fixed contrast Reddish-Greenish (or, magenta-green) stimuli, i.e., stimuli colored with the orthogonal directions to WC or BY. We tested whether warm-cool and blue-yellow show reduced perceptual salience compared to their orthogonal directions. Perceptual salience was measured as the contrast required to achieve perceptual equivalence with a reference stimulus in a grouping task. Lower salience is indicated by higher PSE ratios (> 1.0), meaning more contrast is needed to match the reference. We hypothesized that if adaptation has tuned the visual system to discount frequently encountered chromatic variations, WC and BY axes should show higher PSE ratios than their orthogonal counterparts.

Consistent with prior research, we found that observers in this study exhibited systematic biases along the WC and BY color axes, with both requiring higher contrast than their orthogonal directions to achieve perceptual equivalence. Notably, the magnitude of these biases differed between the two axes. BY showed consistently higher PSE ratios (1.25-1.30) compared to WC (1.03-1.21), suggesting fundamental differences in how these chromatic dimensions are processed. The BY axis ($120^\circ - 300^\circ$ in DKL space) is rotated 30° from the S vs LM cardinal chromatic mechanism (at $90^\circ - 270^\circ$) identified in early visual cortex (Derrington et al., 1984), while the WC axis ($150^\circ - 330^\circ$) positioned at an intermediate angle between the two cardinal mechanisms. Both BY and WC engage combinations of the L vs M and S vs LM cardinal channels, though in different proportions. It could be that because BY is closer to S vs LM that it engages that cardinal axis more than WC.

These findings are consistent with our previous work showing that warm-cool judgements align with saturation asymmetries in uniform color spaces, with the maxima and

minima of warm-cool hues corresponding to directions of weakest predicted saturation (Manalansan, Whitehead, et al., 2025). Results of our previous study using visual search demonstrated that targets were found faster when embedded in warm-cool or blue-yellow backgrounds compared to magenta-green backgrounds, indicating that observers are less sensitive to variations along these axes (Manalansan, Simoncelli, et al., 2025). The current study extends these findings by showing that this reduced sensitivity manifests as higher contrast requirements for perceptual equivalence, with BY showing stronger more stable biases than WC across contrast levels. The differential salience of these axes has implications for understanding how the visual system prioritizes different chromatic information in perceptual grouping and scene segmentation tasks.

We observed different patterns of contrast-dependent changes between the WC and BY conditions. For the WC condition, simple effects analysis revealed a significant linear increase in PSE ratios as fixed contrast increased from 10 to 40, indicating that the magnitude of bias systematically increased with higher contrast levels. The BY condition, on the other hand, showed no significant linear trend across contrast levels, maintaining relatively stable PSE ratios. While absolute PSE values increased proportionally with the fixed contrast in both conditions, the proportional bias (PSE ratios) showed distinctly different patterns. For WC, increasing absolute values with increasing proportional bias suggests contrast-dependent changes in the relative sensitivity between the test and the reference directions. For BY, increasing absolute values with stable proportional bias suggests a more consistent relative sensitivity difference that scales proportionally with contrast level. These different contrast dependencies indicate that WC and BY axes engage underlying mechanisms in chromatic processing. WC shows contrast-dependent changes and BY showing more stable contrast-independent biases.

These observed biases in contrast requirements could potentially be explained by the known properties of the cardinal chromatic mechanisms. However, if our results were due solely to two independent mechanisms tuned to the cardinal L vs M and S vs LM axes, we would predict that any color direction would show biases based simply on its vector component along these cardinal axes. Under this model, directions equidistant from a cardinal axis should show identical biases regardless of their specific angle. Our control experiment measuring the cardinal axes directly was designed to test this possibility; if the biases arose from simple cardinal sensitivity differences, correcting for any scaling differences should eliminate systematic biases for intermediate directions. However, our results cannot be explained by this cardinal model alone. The BY axis at $120^\circ - 300^\circ$ is rotated 30° from the S vs LM axis, while its orthogonal reference at $30^\circ - 210^\circ$ is rotated 30° from the L vs M axis. If higher PSE ratios for BY (1.25 – 1.30) were due simply to lower S vs LM sensitivity, then any direction with similar cardinal axis weighting should show comparable biases. Instead, we found that BY consistently required more contrast than its orthogonal counterpart, despite both directions having equivalent deviations from the nearest cardinal axes. Similarly, the WC axis ($150^\circ - 330^\circ$) and its orthogonal direction ($60^\circ - 240^\circ$) are both positioned 60° from the cardinal axes, yet showed different patterns—WC demonstrated contrast-dependent increases in bias while BY maintained stable ratios across contrast levels.

These systematic differences between test and orthogonal directions indicate that the visual system possesses specialized processing for these specific chromatic axes beyond simple cardinal channel sensitivities. This is consistent with models proposing that ecologically relevant non-cardinal directions engage distinct cortical mechanisms that integrate cardinal inputs in specialized ways (Krauskopf et al., 1982; Solomon & Lennie, 2007).

Similar perceptual biases along non-cardinal chromatic directions have been reported in other studies using different paradigms: reduced sensitivity in visual search tasks (McDermott et al., 2010), asymmetries in uniform color spaces (McDermott & Webster, 2012), and differences in neural responses measured with fMRI (Goddard et al., 2010; Mullen et al., 2015). Our findings extend this work by demonstrating that these biases manifest as systematic differences in contrast requirements for perceptual grouping, with the specific pattern depending on how the test direction engages the underlying cardinal mechanisms.

This study provides converging evidence that warm-cool and blue-yellow chromatic axes have reduced perceptual salience compared to their orthogonal directions, as measured by higher contrast requirements for perceptual equivalence. Critically, our results show that the blue-yellow axis demonstrates greater perceptual bias than the warm-cool axis, indicating that BY is the least sensitive chromatic direction tested. This finding suggests that the visual system shows strongest adaptation along the blue-yellow axis (consistent with this direction capturing the dominant chromatic variation in natural scenes—specifically, changes in daylight from blue sky to yellow sunlight).

Though the scaling for the color space in previous studies (Manalansan, Whitehead, et al., 2025) made use of a different illuminant (Illuminant C), the intermediate bias levels found for the warm-cool axis support our findings that warm-cool judgements align with directions of minimal saturation in perceptual color space. While both WC and BY showed reduced perceptual salience in the current study, the finding that BY demonstrates even lower sensitivity (higher PSE ratios) than WC presents an interesting parallel to our visual search study (Manalansan, Simoncelli, et al., 2025). In that visual search study, we found that targets were detected efficiently when embedded in either warm-cool or blue-yellow backgrounds compared to magenta-green backgrounds, suggesting both axes are perceptually discounted. The current results refine this

finding by revealing that this discounting effect is actually stronger for the blue-yellow axis, consistent with it representing the primary axis of illumination variation in natural scenes. This hierarchy of adaptation—strongest for BY, intermediate for WC, and weakest for magenta-green—demonstrates how chromatic sensitivity is systematically organized according to the prevalence of different color variations in natural visual environments.

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General Discussion

The projects presented in this dissertation provide a picture of a dimension of color tuning, color judgement, and color perception (while thought to be fundamental) is a poorly studied phenomenon, i.e., warm versus cool colors. The first project uncovered the relation between warm and cool hue judgements and color spaces such as DKL and CIELAB as they relate to saturation asymmetries inherently found in these spaces along an orangish-teal direction. The second built upon the first in examining the extent of the biases in saturation with warm-cool and blue-yellow hues compared to their magenta-green counterparts. The third and final project further investigates the perceptual salience of warm-cool and blue-yellow color dimensions compared to magenta-green by determining the biases in contrast to make perceptual judgements and how much more is needed along these warm-cool and blue-yellow dimensions to reach perceptual equivalence compared to magenta-green. Together, the collection of projects presented in this dissertation explored the nature of warm-cool, blue-yellow, and magenta-green hues, judgements, and features.

If adaptation does change with the environment the observer finds herself in, then it is paramount that we disambiguate why the warm-cool (or orange-teal) dimension seems to capture best the direction of least sensitivity in color tuning. Are the very structures of natural scenes actually aligned to blue-yellow or do they differ from context to context? This has yet to be properly uncovered by visual scientists and presents a body of work wanting in the scientific literature. The projects presented here are only the beginning of truly understanding how chromatic adaptation is shaped. There are more studies that can be done to further examine these phenomena, e.g., neuroimaging. Computationally alone, chromaticity and luminance are not the only metrics that perception uses to differentiate between environments. The spatial layout and the objects that populate scenes play crucial roles in how we interact within specific contexts. To

further computational understanding of warm-cool, and adaptation as whole, more complex scene structures have to be taken into account.

With neuroimaging techniques, we can provide a physiological understanding of the encoding processes that underlie visual and chromatic adaptation. Individual differences in the processing of these hues, along with regional, geographic, and cultural differences, may be as important to the perception and representation of warm-cool colors. In essence, visual neuroscience has a bit more to go and I have only scratched the surface of warm versus cool.