



Influence of stimulus size on revealing non-cardinal color mechanisms



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ABSTRACT

Multiple studies have shown that performance of subjects on a number of visual tasks is worse for non-cardinal than cardinal colors, especially in the red-green/luminance (RG/LUM) and tritan/luminance (TRIT/LUM) color planes. Inspired by neurophysiological evidence that suppressive surround input to receptive fields is particularly sensitive to luminance, we hypothesized that non-cardinal mechanisms in the RG/LUM and TRIT/LUM planes would be more sensitive to stimulus size than are isoluminant non-cardinal mechanisms. In Experiment 1 we tested 9–10 color-normal subjects in each of the three color planes (RG/TRIT, RG/LUM, and TRIT/LUM) on visual search at four bull's-eye dot sizes (0.5°/1°, 1°/2°, 2°/4°, and 3°/6° center/annulus dot diameter). This study yielded a significant main effect of dot size in each of the three color planes. In Experiment 2 we tested the same hypothesis using noise masking, at three stimulus sizes (3°, 6° and 9° diameter Gabors), again in all three color planes (5 subjects per color plane). This experiment yielded, in the RG/TRIT plane, a significant main effect of stimulus size; in the RG/LUM plane, significant evidence for non-cardinal mechanisms only for the 9° stimulus; but in the TRIT/LUM plane no evidence for non-cardinal mechanisms at any stimulus size. These results suggest that non-cardinal mechanisms, particularly in the RG/LUM color plane, are more sensitive to stimulus size than are non-cardinals in the RG/TRIT plane, supporting our hypothesis.

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1. Introduction

It has been estimated that humans can perceive millions of different hues (e.g., [Linhares, Pinto, & Nascimento, 2008](#)). How can we organize these colors, and how does the brain process them?

The colors that we perceive can be represented in a three-dimensional color space (see [Fig. 1](#)) with the axes representing the opponent color preferences of the retinal ganglion ([Dacey & Lee, 1994; Kaplan, Lee, & Shapley, 1990; Kolb, 1991](#)) and lateral geniculate nucleus (LGN) cells ([Derrington, Krauskopf, & Lennie, 1984; DeValois, Abramov, & Jacobs, 1966; Kaplan et al., 1990](#)): red versus green (RG), bluish/violet versus yellowish/chartreuse (a.k.a. tritan, TRIT), and black versus white (a.k.a. luminance, LUM). The independence of these axes has also been demonstrated psychophysically, first by [Krauskopf, Williams, and Heeley \(1982\)](#). This color representation is often referred to as the DKL color space, after the pioneering neurophysiological work by [Derrington et al. \(1984\)](#), or sometimes MBDKL color space to also include the psychophysical color space of [MacLeod and Boynton \(1979\)](#). These

three axes are referred to as the *cardinal axes*, and the neurons that register these colors as the *cardinal mechanisms*.

All colors other than the cardinals, such as orange, burgundy, and sky blue, are known as *non-cardinal colors*. Neural mechanisms underlying these colors do not emerge until the cortex ([Gegenfurtner, 2003](#)). However, evidence for the existence of mechanisms specifically tuned for non-cardinal colors is mixed. Most studies are able to find evidence for such mechanisms in the isoluminant (RG/TRIT) color plane. But evidence for non-cardinal mechanisms in the two planes containing luminance (RG/LUM and TRIT/LUM) is weaker. We will first review evidence for non-cardinal mechanisms in each of three planes of color space, and then we will propose our hypothesis that the two planes containing luminance may be more sensitive to stimulus size.

In the isoluminant color plane, evidence from multiple psychophysical techniques supports the existence of specific non-cardinal mechanisms. Note that the studies reviewed here are only a sample of such studies, not an exhaustive summary. (For additional studies of non-cardinal mechanisms, see [Gunther \(2014a\)](#) for a summary table and [Eskew \(2009\)](#) for an extensive review.) One of the first studies to support the existence of separate mechanisms underlying the non-cardinal colors was that of [Krauskopf, Williams, Mandler, and Brown \(1986\)](#). Although [Krauskopf et al.](#)

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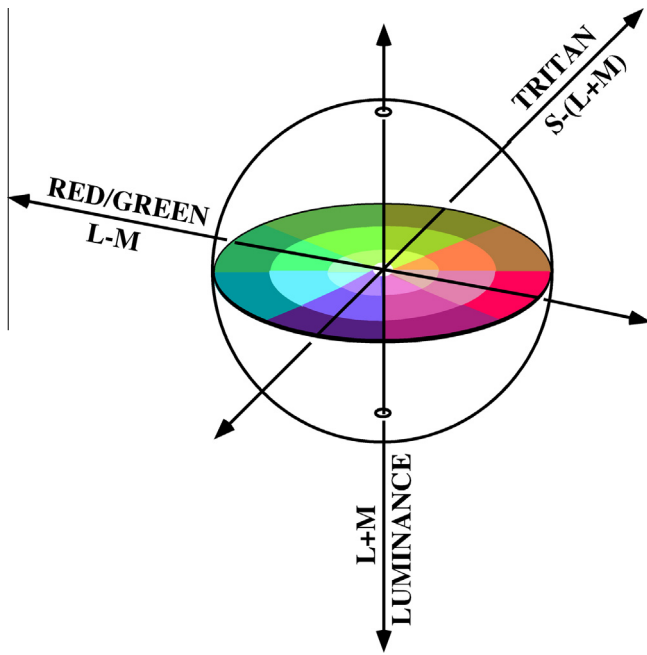


Fig. 1. Derrington-Krauskopf-Lennie three dimensional color space. Cone inputs are shown on axes: L = long-wavelength-sensitive; M = medium-wavelength-sensitive; S = short-wavelength-sensitive. Reprinted from Vision Research, Vol. 43, K.L. Gunther and K.R. Dobkins, Independence of mechanisms tuned along cardinal and non-cardinal axes of color space: Evidence from factor analysis, pp. 683–696. Copyright 2003. In color online.

(1982) interpreted their own results as supporting the existence of primarily only the three cardinal mechanisms, Krauskopf et al. (1986) conducted a Fourier analysis of the data of Krauskopf et al. (1982) and found clear non-cardinal peaks in the second harmonic. In addition, in a detection and discrimination experiment, Krauskopf et al. (1986) found that non-cardinal stimuli were discriminated as well as were cardinals, supporting the existence of separate non-cardinal mechanisms. Webster and Mollon (1991, 1994) exposed their subjects to adapting stimuli modulated along each of a number of different directions in color space. Following adaptation, sensitivity to the adapted direction was reduced, but sensitivity to the orthogonal direction was mostly unaffected. They saw similar results whether the adapting axes were oriented in cardinal or non-cardinal directions. If only cardinal mechanisms exist to detect color, a non-cardinal adaptor should have fatigued both the RG and TRIT cardinal mechanisms, thus reducing sensitivity in all directions in the color plane. However, selective adaptation to the adapted non-cardinal axis with sparing of sensitivity to the orthogonal non-cardinal axis suggests the existence of non-cardinal color mechanisms. Stoughton, Lafer-Sousa, Gagin, and Conway (2012) found similar results following adaptation in macaque subjects. Using a different paradigm, Krauskopf, Wu, and Farell (1996) looked at the coherence of plaid stimuli. Plaids are composed of two superimposed sinusoidal gratings, oriented 90° apart from each other, drifting perpendicularly to the orientation of their stripes. The theory underlying the use of these stimuli holds that if the two component gratings tap the same underlying neural mechanisms, they cohere into a plaid that appears to drift as a single object. If, instead, the two component gratings tap separate underlying mechanisms, the gratings appear to slip across one another. If the two component gratings are non-cardinal colors, such as orange/turquoise and purple/lime, they might both tap the underlying cardinal RG and TRIT mechanisms and thus the plaid would cohere. Alternately, they could tap separate

non-cardinal orange/turquoise and purple/lime mechanisms and thus slip across one another. Krauskopf et al. (1996) found that the latter occurred, non-cardinal components slip, thus supporting the existence of separate underlying mechanisms for non-cardinal colors. Li and Lennie (1997) used noise masks as their stimuli – patches of color embedded in pixelated noise. If the color patch and the noise are detected by separate mechanisms, the stimuli can be easily detected. All three of Li and Lennie's subjects could detect purple/lime (which they called purple/yellow-green) patches when embedded in orange/turquoise (which they called orange/blue-green) noise at the same contrast as when unmasked. One of their three subjects could easily detect orange/turquoise patches when embedded in purple/lime noise – the other two subjects required higher contrast stimuli when embedded in noise as compared with unmasked thresholds. Hansen and Gegenfurtner (2006) also examined the effects of noise on stimulus detection, but with four non-cardinal directions (30° , 60° , 120° , and 150° between the cardinals), rather than the two (45° and 135° between the cardinals) that Li and Lennie tested. They, too, found evidence for separate non-cardinal mechanisms in all directions tested. This was true whether they used a single noise direction, or whether they bracketed the signal direction with two-sided noise. In a visual search study (Gunther, 2014b), subjects searched for bull's-eye targets from one color axis in amongst bull's-eye distractors from the orthogonal color axis. Non-cardinal visual search is facilitated by the existence of separate underlying mechanisms for each non-cardinal axis. If such mechanisms do not exist, both cardinal mechanisms in the plane being tested (e.g., RG and TRIT) will respond to both the target (e.g., orange/turquoise) and the distractors (e.g., purple/lime). In the isoluminant plane, Gunther's subjects performed equally well on cardinal (RG vs. TRIT) and non-cardinal (orange/turquoise vs. purple/lime) visual searches, supporting the existence of separate non-cardinal mechanisms. McDermott, Malkoc, Mulligan, and Webster (2010) found that visual search of an orthogonally-colored target was facilitated when subjects adapted to the distractor/background color axis, more than when subjects adapted to the target color axis. This was true for cardinal and for non-cardinal axis pairings. In one contradictory study, a factor analysis on contrast sensitivity data, Gunther and Dobkins (2003) failed to find evidence for non-cardinal mechanisms in the isoluminant plane. This could occur if the mechanisms are separable, as determined by the other psychophysical techniques above, but not entirely independent and instead partially intercorrelated. In summary, the majority of the evidence supports that there are strong non-cardinal neural mechanisms in the isoluminant plane.

Non-cardinal mechanisms seem to be less strong in the RG/LUM and TRIT/LUM planes. Webster and Mollon (1991, 1994) found mixed adaptation effects for non-cardinal stimuli in these two planes, with some subjects showing good selective adaptation (e.g., an intense-red/dim-green adaptor does not affect detection of an intense-green/dim-red stimulus), but other subjects showing crossed adaptation. In their plaid coherence experiment, Krauskopf et al. (1996) found that plaids comprising orthogonal non-cardinal component gratings in the RG/LUM and TRIT/LUM planes tended to cohere, not slip. This implies that the non-cardinal components were both detected by the cardinal mechanisms (i.e., RG and LUM, or TRIT and LUM depending on the color plane), rather than there being separate neural mechanisms underlying the perception of non-cardinal stimuli in these two color planes. Similarly, in Li and Lennie's (1997) noise masking experiment, they found that noise masks in the two 45° non-cardinal directions in these color planes equally masked both non-cardinal directions, arguing against separate non-cardinal mechanisms. And finally, in Gunther's (2014b) visual search paradigm, subjects performed

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