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Cortical double-opponent cells and human color perception

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Human color perception's dependence on the spatial pattern of color is a function of color contrast. At low color contrast, the visual system acts as a spatial integrator of color signals. Therefore, near threshold, the optimum color pattern is a large, uniformly colored region. But the system changes at high color contrast, becoming more sensitive to changes in the spatial context of color especially color boundaries with surrounding regions. We offer a mechanistic explanation of these phenomena in terms of the contrast dependencies of single-opponent and double-opponent neurons in the primary visual cortex, V1.

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Introduction

Let us begin with our most important opinion about color perception: that human perception of color is entangled inextricably with pattern and object perception. That is, color is not painted onto the visual scene that is perceived independently of the colors, as often has been supposed in the past. Rather, " . . . space and color . . . are interdependent aspects of a unitary process of perceptual organization." [1]. Our opinion is based in part on the neurophysiology of color vision (e.g. in Ref. [2]). But our view also is based on perceptual phenomena that reveal the powerful influence of spatial pattern on the color perceived. A second opinion we offer here is that color contrast affects how pattern influences color. At low color contrast, near color threshold, the visual system perceives color by summing incoming signals over a wide region of the visual image. However, it perceives high-contrast, very visible color patterns differently, deriving surface colors from signals at the boundaries of surfaces. Therefore, the results of color perception studies have a great lesson to teach all vision research: supra-threshold vision can be very different from vision at threshold.

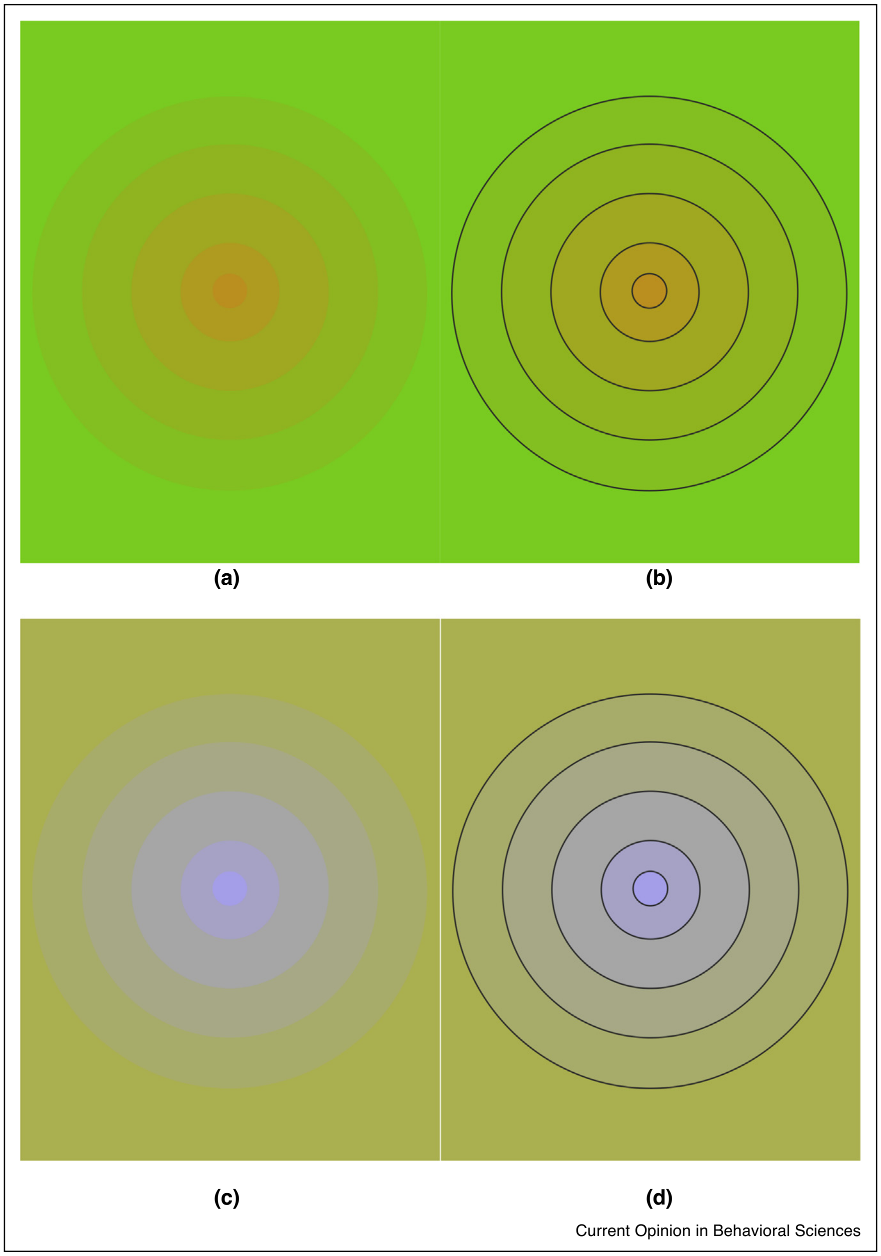
Color edge demonstrations

Let's consider two examples

First, look at the Chevreul illusion [3] in color, studied by Daw [4]. Figure 1a is an example of a color Chevreul illusion. It is composed of concentric, uniformly colored annular regions (in which the colors run from green to orange–red). The concentric ribbons are approximately equal in luminance and vary stepwise in color. Even though the concentric ribbons are physically uniform in their spectral properties, the color appears to change gradually from inner to outer edge of each ribbon. The color of each circular ribbon appears redder near the outer boundary and greener near the inner boundary. In Figure 1b all edges between colored regions have been outlined with black circular lines, and the Chevreul illusion disappears; there is no color shading. Of course, the spectral properties of the ribbons are unchanged by the presence or absence of the black outlines in Figure 1 and it is obvious to the viewer that the concentric ribbons are spatially uniform in color in Figure 1b. The comparison of Figure 1a with b indicates that color edges are important in producing the color-Chevreul illusion in which color spreads across a region from its edges. Figure 1a,b is drawn with color contrast that will drive only the L-cones and M-cones. Such figures are likely to stimulate cells in the visual cortex that receive excitatory drive from the Parvocellular pathway—the Red–Green pathway [2]. Figure 1c,d shows the Chevreul illusion, and its outlined control, in a Blue–Yellow (S-cone isolating) color direction; Figure 1c,d reveals that color contrast at edges also is crucial for color perception when the only information about color is being carried by cortical cells driven by S-cone signals.

A second demonstration of the power of color edges for influencing color perception is what happens when one smears out the edge in visual space so that the color change is gradual instead of abrupt, as in Figure 2. There is a blue–green (equiluminant) color disk on a gray background in Figure 2a. Then in Figure 2b, we spatially blended the color of the color target with the gray background disk; the fraction of color is a linearly decreasing function of the distance from the edge of the target. But the spectral properties of the pixels in the central region of Figure 2b,

Figure 1

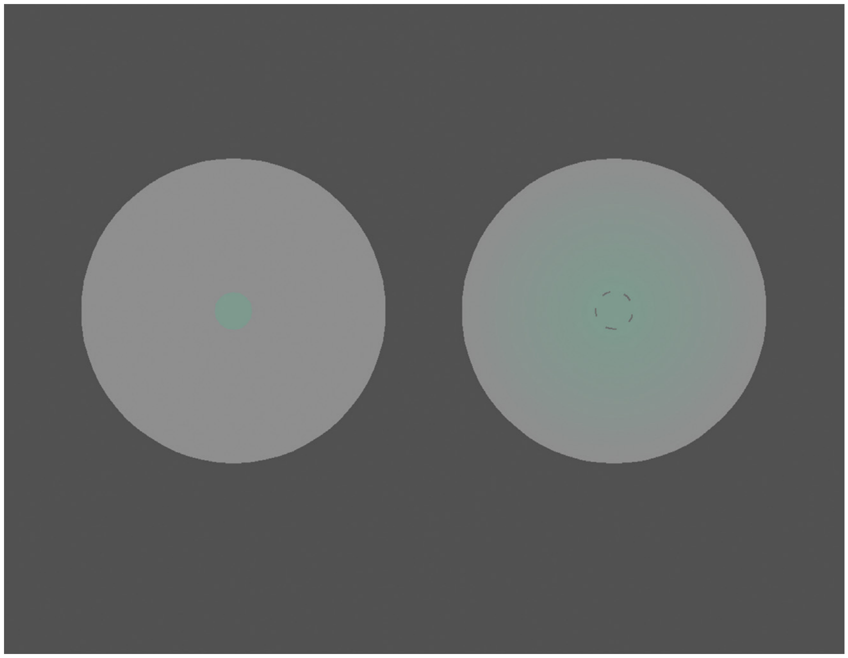


Color Chevreul pattern.
(a) In this example of a Chevreul illusion, a series of concentric rings surrounds a central circle. From the inner circle to the outermost ring, the color changes in even steps, ring to ring, from the central orange to the outer green. Even though each ring is uniformly colored, for a given ring its inner edge seems to be greener whilst its outer edge seems more orange. **(b)** The same pattern from (a) is overlaid with a series of black circles corresponding to the edges of each concentric ring. The illusion disappears and one can now see clearly that the interior of each ring is spectrally uniform. **(c)** Similar to (a) except that color modulation is such as to isolate the S-cones. **(d)** Similar to (b) but with the S-cone isolating colors.

the region marked by the gray dashed lines, are identical to those of the disk in Figure 2a. The vividness of the color, its saturation, is apparently much greater in Figure 2a, the target with the sharp edge. Also, what is clear is that the perceived color depends on the spatial pattern not just the local spectral properties of the target region.

The powerful effect of edges on color perception is consistent with a large body of work that indicates that color perception depends on spatial context [5,6]. One example is filling-in of color in stabilized images across long distances from an unstabilized boundary [7]. Color filling-in in the periphery of the visual field can be seen

Figure 2



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Sharp edge versus smeared edge in color.
At the center of the left-hand gray circle is a small greenish-blue circle. The edges of the colored circle are sharp. In the right-hand gray circle, the same central circle now has its color extended outwards and blended gradually into the background gray, so that there are no sharp edges in color. The dashed circle is a guide to the eye to help the reader see that the central circle on the right is the same as the circle on the left. The left-hand sharp circle appears more colorful (more saturated) than the right-hand edgeless cloud of color.

even with voluntary fixation [8,9]. These perceptual results suggest that the color appearance of a region may be more dependent on color contrast at the boundary of the region than it is on the spatially integrated spectral reflectance of the region's interior.

The strong influence of surrounding regions on the color of a target region has been known for a long time [10]. Color and form interact through the contrast that surrounding forms exert on the target region. Color contrast effects are assumed to be involved in the experience of color constancy [11] and also in the induction of color into a neutral target by a surrounding color context [12–15]. Previous research suggests that V1 may play a role in color induction caused by color contrast. For instance, the color tuning curve of single neurons in macaque monkey V1 was changed on different color backgrounds in a manner consistent with human color perception of color induction [16].

With Figures 2 and 3 and the experiments reviewed below, we are extending the view that color edges are important for color induction and color constancy. Now we propose that the color we perceive in color targets on neutral backgrounds is dominated by color signals at the edges of the targets. We must add the proviso that the dominance of edges occurs in suprathreshold color vision when color can be seen clearly.

What is the functional reason that color appearance is so dependent on the colors of the near surroundings, on the edges? One likely justification is that the brain constructs a color signal to try to recover the reflective properties of surfaces that are independent of illumination. To accomplish this task, the neural mechanisms of color perception need to make comparative computations—local subtractions across object boundaries—that take into account the spatial layout of the scene as well as the spectral reflectances of target and surrounding surfaces [11,17,18].

Color vision as a spatial integrator

Contrary to all the evidence about the importance of color edges, it is generally believed that when the brain does its computations that lead to color perception, it is most influenced by large regions of color or by color patterns of low spatial frequency. In other words, color perception is supposed to be a spatial integrator. The reason for this belief is the powerful influence of the results in the classic paper by Mullen [19]. Mullen measured sensitivity (1/detection threshold) for sinusoidal, colored grating patterns that were equal in luminance (equiluminant) with the background. The gratings in Mullen's study were defined only by color contrast. Best detection was at the lowest spatial frequency for both red–green and blue–yellow grating patterns. That is, color detection was low pass. There are many psychophysical studies that support the concept of low-pass color perception. For example, Poirson and Wandell [20,21] fit large datasets they collected on color appearance and color detection with two low-pass color mechanisms, one for red–green and one for blue–yellow, and one band-pass luminance mechanism. It is important to note about the Poirson–Wandell studies that they used square-wave patterns with sharp edges so that their low frequency patterns in fact contained a large amount of spatial energy at higher spatial frequencies. Therefore, the responses they measured were not in fact evidence for the low pass chromatic mechanisms they deduced from their data. Another example: Gowdy *et al.* [22] reported "two sides of the chromatic split field are detected essentially independently by red or green 'blob' detectors." In a commentary to a book chapter, Hans Irtel wrote, "It is well-known that there is a fundamental difference between the achromatic and chromatic system in the spatial domain: the chromatic system behaves like a spatial low-pass filter while the achromatic system behaves like a spatial band pass" [23].

All the solid evidence for a spatial lowpass color system, like Mullen [19] and Gowdy *et al.* [22], was obtained at detection threshold. The demonstrations offered in Figures 1 and 2 and the evidence reviewed above about color contrast and context come from experiments done on visible, supra-threshold color patterns. The inescapable conclusion is that the human color perception changes fundamentally with color contrast. We offer an explanation for this transformation with contrast. Our hypothesis is that there are two separate visual systems that contribute to perception. One is more sensitive to color contrast and dominates perception of color at low color contrast while the other system's response grows more steeply with color contrast so that at supra-threshold contrast the second system predominates.

Color saturation of checkerboards and large uniform squares

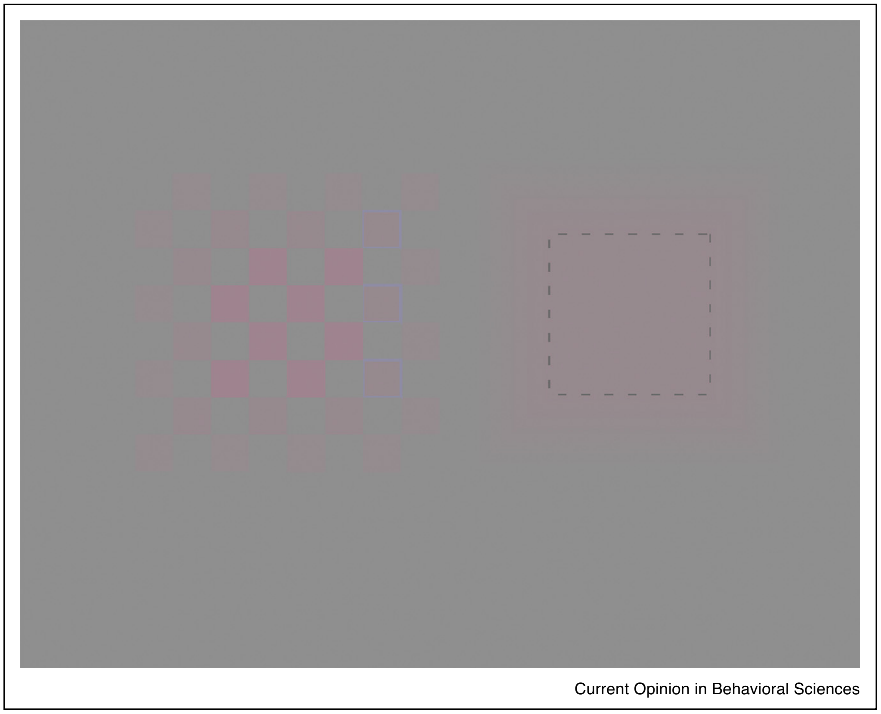
We designed an experiment to test the two-mechanisms hypothesis [24••]. The idea was to measure color saturation for different spatial patterns as color contrast increased from near threshold to highly visible levels. We measured perceived saturation with the method of saturation scaling [25]. The two patterns used were a fine checkerboard pattern composed of equiluminant red and gray checks, and a large uniform square. In the experiments the fundamental spatial frequency of the checkerboard was around 2 c/deg which was chosen to isolate the perceptual mechanism that responds best to color patterns. A diagram of the kind of stimuli used is shown in Figure 3; that figure is also a demonstration of the main effect. The checkerboard pattern on the left and the uniform square on the right (delineated by the dashes written on top of the pattern) have the same space-averaged cone contrast, where cone contrast is computed by comparing the cone activation produced by each pattern to that produced by the gray background that was present before stimulus presentation. If supra-threshold color perception was determined by a spatial averaging mechanism, the apparent color saturations of the two stimuli should be identical. But they are not identical in the demonstration in Figure 3; the checks in the checkerboard appear much more saturated. And they are not identical in the data in Figure 4 [24••]. As cone contrast rises, the perceived saturation of the checkerboard climbs much more steeply than that of the large uniform square. Articulated color patterns are much more colorful than large expanses of uniform color, surprisingly disconfirming the color integrator hypothesis for suprathreshold color perception.

The two mechanisms that are in play are by hypothesis related to the single-opponent and double-opponent cortical cells that have been found in primary visual cortex, V1 [26–31]. All color-responsive neurons in V1 can be subdivided into single-opponent and double-opponent categories [28,29,32]. Single-opponent cells are spatially low pass and also untuned for orientation [28,31]. Double-opponent cells are tuned for both spatial frequency and orientation and respond best to patterns in the 2 c/deg range [29,31,32]. We hypothesize that at low cone contrast the single-opponent cells are most sensitive but that their response grows much less with cone contrast than does the response of double-opponent cells. Considering the physiological data (e.g. in Refs. [29,31]), the uniform square is a good stimulus for single-opponent cells while the fine checkerboard pattern selects for double opponent cells. This could explain the results in Figure 4. The perceived color of the uniform square grows so little with cone contrast because, we infer, single-opponent response grows little with contrast. The perceived saturation of the checks in the checkerboard grows more steeply with contrast because the percept is derived from the activity of double-opponent cells that, by hypothesis, becomes much larger at higher cone contrast. Future studies of visual cortical neurons could test these ideas directly.

Color edge detectors

Other recent work on color perception supports the concept that supra-threshold color vision is spatially tuned, not low pass. One paper utilizes the method of classification images to map out the spatial profiles of the spatial mechanisms that respond at equiluminant color edges [33••] and compares those edge mechanisms with

Figure 3



Demonstration of a checkerboard compared to a large uniform object.

In this figure a central red–gray checkerboard (left) and a central red square (right) are both extended outwards and blended gradually to fade to the background gray color. The dashed-lines are a guide indicating the edges of the original central square. Compared to the gray background, the colors of the square and checkerboard have the same space-averaged cone contrast. However, the checkerboard appears more colorful.

the edge detectors for black–white, achromatic patterns. The derived color edge-responsive mechanisms are spatially differentiating and resemble the black white edge-responsive mechanisms closely. We avoid the term edge detectors so as not to suggest that these edge-responsive mechanisms are responsible for chromatic detection; they are supra-threshold mechanisms. The spatial profiles of the color edge mechanisms derived in these psychophysical experiments resemble the spatial sensitivity profiles of double-opponent cortical neurons described in Ref. [31]. The edge responsive mechanisms revealed in the results of McIhagga and Mullen [33••] could support the perceptual results in the demonstrations shown in Figures 1–3

Color spatial filtering

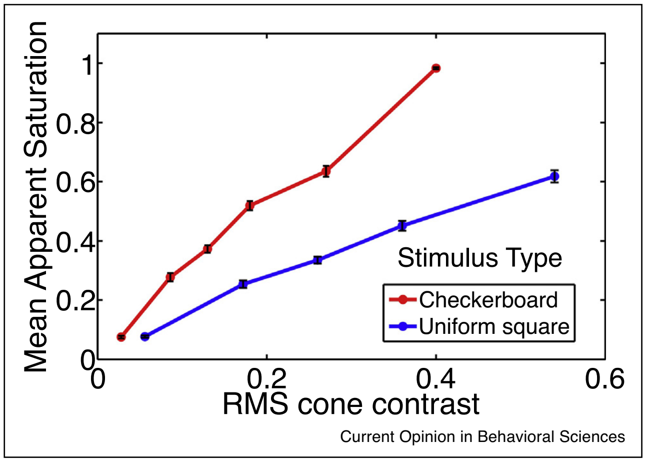
Another recent paper offers an explanation of color contrast in human perception in terms of spatial filtering of the color signals [34••]. The problem spatial filtering solved in this case was the appearance of the Kitaoka Tomato illusion: why does a tomato still look red when viewed through a green filter (as presented on Kitaoka's Twitter account, https://twitter.com/AkiyoshiKitaoka/status/837825700816027648). Kitaoka's Tomato is a clever demonstration of color constancy but the phenomenon is the same as in many classic examples of color constancy (e.g. [10,17]). What Shapiro *et al.* showed [34••] was that if one spatially filtered each of the RGB primaries used to make the color image, one found that the high pass filtered image looked like the color pattern in plain view. That is, spatial filtering removed the common color signal of the illumination and left the color pattern.

In the biological visual system, the neurons cannot spatially filter the RGB primaries in the way that Shapiro *et al.* [34••] did, but visual cortical neurons can spatially filter the cone responses. That is basically an operational description of the signal processing by single-opponent and double-opponent cortical cells in V1 [29]. Therefore, the results of Shapiro *et al.* [34••] suggest that the two-mechanisms hypothesis will be sufficient to explain the appearance of Kitaoka's Tomato and related patterns. Dixon and Shapiro [35] previously suggested that spatial filtering of color signals could help explain the phenomenon of the Color Dress that went viral on the Internet in February 2015 (note – the dress and its story are also provided in Ref. [35]).

Evidence for low pass color vision?

A recent paper supporting the low pass view of color vision came from Tyler and Solomon [36••]. They used a

Figure 4



Normalized saturation scaling data averaged across nine observers, presented as a function of root-mean-square cone contrast for a red–gray checkerboard (red line) and a uniform red square (blue line), where each was presented separately on an equiluminant gray background. Error bars represent ±1 SEM. The stimuli were each $10^\circ \times 10^\circ$ in spatial extent, and the checkerboard consisted of 32×32 checks, so that its dominant spatial frequency was 2.26 c/deg. Each pattern appeared for 0.5 s and then disappeared, at which time the participant rated the color saturation [24••]. Note that the cone contrast of the uniform square was scaled to take into account the fact that the space-averaged cone contrast of the red–gray checkerboard was one-half that of the uniform square of the same chroma/cone contrast (compared to the equiluminant gray). Figure reproduced from Ref. [24••].

series of demonstrations to support their ideas that color perception is basically a low pass system. One of their demonstrations was aimed at refuting the results of Krauskopf [8] that a blurred color pattern will fade and disappear. Tyler and Solomon manufactured patterns somewhat like Figure 2b, and asserted that they did not disappear as Krauskopf [8] claimed. We believe the discrepancy may be caused by the spatial scale and/or cone contrast of the patterns used. But what Tyler and Solomon did not do is to compare the blurred color patterns with a sharp-edged pattern of the same chromaticity as we have done in Figure 2a,b. They would have seen that the color is much degraded in the blurred pattern.

Another demonstration in Tyler and Solomon [36••] is a set of color and black/white swept grating patterns derived from images from Jim Kasson's blog, http://blog.kasson.com/the-last-word/chromaticity-csfs/. The first (black/white) swept grating pattern was manufactured by John G. Robson in the 1960s and was published first in Floyd Ratliff's book Mach Bands [3]. Tyler and Solomon [36••] drew attention to the fact that at low color contrast, the response to the colored swept grating pattern is low pass. This result is not in conflict with our working hypothesis because at low color contrast near detection threshold, we expect the low pass mechanism to dominate. The swept color gratings in Kasson's blog support the idea that at higher color contrast more color is perceived at intermediate spatial frequencies. That is, when color patterns are clearly visible, a spatially tuned color mechanism determines how much color we see.

Conclusions

Human color perception is spatially low pass at very low color contrast near threshold. At higher color contrast when color patterns are clearly visible, color perception is not low pass but edge-sensitive, or in other words, spatially tuned. The edge sensitivity of color has been known for a long time to influence color constancy [10] and color induction [37] but now we point out that it also determines the perceived color of colored objects on neutral backgrounds, that is, all color perception of surfaces and objects. Our working hypothesis that explains the dual nature and the contrast dependence of color perception's spatial properties is the two-mechanism hypothesis. This hypothesis proposes that cortical double-opponent cells in V1 play a major role in the perception of the color of surfaces and objects when we see the color clearly. Another conclusion that transcends the topic of color perception is that in general one cannot assume that the spatial properties of perception at threshold are the same as they are suprathreshold.

Conflict of interest statement

Nothing declared.

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