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The Verriest Lecture: Color vision from pixels to objects

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Scientific investigations of color have traditionally used a pixel-by-pixel approach. By determining the cone excitations of each point in an image, images can be exactly reproduced on different devices by generating metamers. The cone excitations can be used to derive estimates of color appearance under simplified viewing conditions. However, the primary purpose of color perception is not to generate a copy of our surrounding world in our brains. Instead, I propose that color is highly suitable for detection and recognition of objects in our environment, and that it is an entire distribution of color coordinates within an object that defines its color appearance. Here, I review the behavioral, neural, and computational mechanisms underlying object and color processing in the natural world.

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1. INTRODUCTION

The investigation of human color vision has been enormously successful for centuries. The epochal insights of Newton [1] and Young [2] were substantiated by Maxwell [3] and Helmholtz [4], formalized [5–7], and eventually yielded universally accepted industrial standards [8–10]. As of now, the photoreceptor sensitivity functions are precisely tabulated [11], and their neural and even genetic basis is well understood [12,13]. This first stage of color vision, at the contact of photons with receptors in the eye, forms the basis for any kind of color reproduction, such as in the color displays in TVs, computers, and smartphones that permeate every aspect of our daily lives. A second stage of processing, in color-opponent channels of the retina, was first suggested by Hering ([14]; but see Ref. [15]) and has been thoroughly characterized in behavior [16], physiology [17–23], and computation [24–26]. Opponent color mechanisms are crucial for color discrimination and adaptation [27–29]. For a standard human observer, we can calculate the cone excitations at the first stage and the cone-opponent signals at the second stage. These numbers can be used to perfectly reproduce any image. However, the goal of the visual system is not to reproduce the outside world in our heads. Rather, its primary goal is to recognize objects, scenes, and people and to guide our interactions with them [30].

Surprisingly little is known about what happens to the color signals in the brain, where visual signals are processed from a pixel-like to an object-based representation (see Fig. 1). The world of cone sensitivities and color opponency represents flat, matte surfaces as single points in the color space. Models predicting the appearance of color have also used such flat, matte representations of the world, assuming that the environment can be described as an equivalent surround and a background (for reviews, see Refs. [31,32]). But our world consists of complex 3D objects that combine shape, color, and material and form whole distributions in the color space [33–36]. The most important functions of color (and perception in general) are related to objects. Color helps us see things quicker and remember them better ([37,38]; for a recent review, see Ref. [39]). We think it is time to go beyond past achievements and to fundamentally rethink color from an object-oriented perspective.

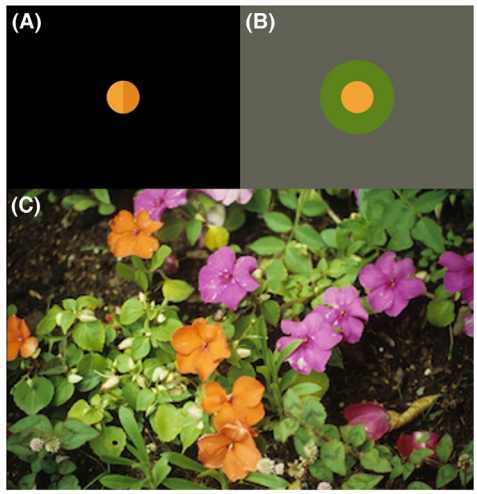

Fig. 1. (A) Traditionally, cone mechanisms were investigated using split fields on a dark surround and (B) color appearance with patches of light in a surround of a different color on a neutral background. This approach is far from the goal of understanding how we see (C) colored objects in natural scenes.

2. WHAT IS COLOR GOOD FOR?

Here, I propose the viewpoint that color is fully integrated with spatial vision and plays an eminent role in our perception of the world. While this viewpoint was promoted 40 years ago, supported by a tremendous amount of data [40], the Zeitgeist pushed it aside and gave way to what has been termed the "coloring book theory of visual perception" (for a critical evaluation, see Refs. [41,42]). The assumption is that spatial form and color are processed completely independently in parallel pathways from retina to extra-striate cortex. A luminance-based system would do all the heavy lifting, from delineating edges and recognizing objects to estimating their positions and calculating movements [43–46]. The color vision system would then, at a leisurely pace, fill in the regions, presumably for the aesthetic pleasure of the viewer. Evidence for this peculiar view of color came from several sources. First, there were a whole lot of demonstrations that showed impairments of perception when stimuli were defined by chromatic contrast exclusively (e.g., Refs. [47–49]). Second, electrophysiological recordings showed neurons tuned to color but not to form or motion, localized in certain cortical regions that could be identified anatomically [47,48,50,51]. Third, in experiments on object recognition, performance for full-color images was not better than for line drawings [52]. Fourth, information transmission on color TVs could get away with a very limited bandwidth for color, compared to luminance (e.g., Refs. [53,54]).

History has shown that the above findings were not as clear-cut as originally thought. I will present some aspects in more detail below and give a brief overview here. First, isoluminant stimuli not only get rid of luminance contrast, but due to the vast overlap in L- and M-cone spectral absorptions, the overall possible contrast range becomes very limited. When quantitatively comparing color stimuli and matching luminance stimuli at an equivalent contrast in the cone photoreceptors, no deficit was found at isoluminance (for reviews, see Refs. [55,56]). Second, in quantitative single-unit recordings, only a modest degree of segregation between sensitivities to color, form, and motion was measured (for reviews, see Refs. [55,57]). Third, when studying object recognition, usually isolated objects were shown, and line drawings even go one step further in extracting the most important object edges. And fourth, it is indeed the case that chromatic sensitivity is not very good at the very high spatial frequencies, thus allowing a lower information transmission rate [58–60]. However, this does not in any way impede the important role of color information at low and medium spatial frequencies.

Indeed, color has been shown to aid us in seeing things quicker and remembering them better [37–39]. This is in line with the fact that color has been shown over and over again to be one of the most important attributes for rapid visual search (see Refs. [61,62]). Color aids in object recognition [63,64] by facilitating fast visual encoding [37,65,66] and memory retrieval [37,38]. In the experiments by Wichmann *et al*. [38], observers had to remember a series of natural images, half of which were presented in color and the other half in grayscale. For testing, the images were interleaved with new images, also in color or grayscale, and the observers had to indicate whether a given image was new or old. Observers were between 5% and 10% better for the color images, irrespective of the original presentation duration, which could be between 50 and 1000 ms. These experiments were also done on a sample of color-deficient observers [67]. Quite unexpectedly, the same absolute levels of performance were observed, and the same 5%–10% difference in performance. When color-normal, trichromatic observers were shown images that had red–green modulations removed, a deficit emerged [68]. It seems that color vision-deficient observers have learned to compensate for their reduced color information in visual memory.

The above results indicate that color already helps recognition at the shortest presentation duration of 50 ms. This is in disagreement with the idea that color vision is a slow process. However, in these experiments, no mask was presented, and this allows for visual processing to go on for several hundred milliseconds in iconic memory [69,70]. We therefore devised experiments to specifically explore the dynamics at the very briefest exposure durations in more detail [37]. We used a match-to-sample task, where ultrabrief presentations (16–64 ms) were followed by a mask. Then the target image was presented together with a distractor image from the same semantic image category, and the observer had to indicate which image matched the one they had first seen. The mask was specifically designed to mimic the properties of natural images and the color distributions of target and distractor. Again, images could be presented in color and in grayscale, and testing was done in color and grayscale. We also included a crucial new condition, where images were first presented in color and then tested in grayscale. Performance turned out to be better for color for all presentation durations. However, at the shortest presentation duration of 16 ms, performance was better for color irrespective of whether the testing was done in color or in grayscale. Under that condition, presumably low-level sensory factors are beneficial for color, and these lead to a better encoding of the color images. This result is in accordance with color aiding the segmentation process [65,66]. At the longest presentation duration of 1000 ms, color was still better than grayscale, but only if presentation and testing were done in color. This allows for using an extended memory representation for the color images that would then improve retrieval of the images from memory. For example, if something violet is seen in the image, it can be used to distinguish between the target and the distractor. This is, of course, not possible when the testing is done in grayscale. A smooth transition between the two regimes was found at intermediate presentation durations. The slightly longer processing it takes for grayscale images is in line with findings of slightly longer fixation durations when viewing images in grayscale versus color [71,72]. Color would be most important when objects are otherwise more difficult to identify. This would be for the very brief presentations used in the above experiments, but it could also be in conditions of partial occlusion, as illustrated in Fig. 2. Akin to conditions where trichromatic primate color vision evolved, the ripe red fruit is much easier to spot among the green leaves when red–green chromatic information is present.

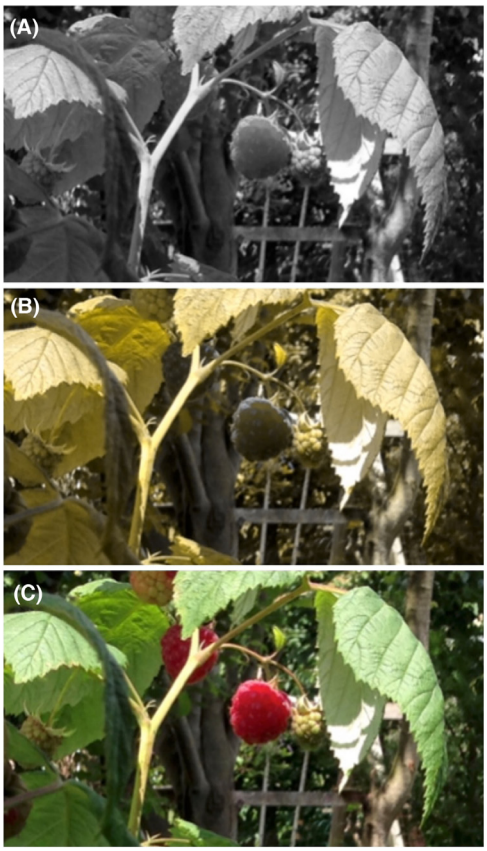

Fig. 2. Raspberries among green leaves. (A) Grayscale image, (B) simulation of what the image would look like to a color vision-deficient observer with deuteranopia, and (C) original color image. Only in the full-color image, a second red but occluded raspberry becomes visible.

3. IT'S ALL ABOUT HUE

Color is a three-dimensional property that can be described by an arbitrary set of three independent dimensions. This freedom of choice has been used extensively in the past and led to the usage of a large number of different color spaces, from physiologically based spaces that specify color in terms of photoreceptor activations, to cone-opponent spaces that span a hue circle at one or more intensity levels, to device-dependent spaces that are widely used for display or printing. While all of these spaces are mathematically closely related or even equivalent, a plethora of color spaces certainly complicates communication about color phenomena. It can also have dramatic effects on sampling. In cone excitation or cone contrast spaces, all possible colors get mapped to a small region of the 3D color space because, for evolutionary reasons, the correlations of the L- and M-cone absorptions are extremely high, and the correlations with S-cone excitations are also quite significant. In cone-opponent diagrams, these dimensions are essentially decorrelated [24–26]. Some of these spaces, such as the DKL color space proposed by Derrington *et al*. [21] or the chromaticity diagram proposed by MacLeod and Boynton [73], have axes that mimic the transformations of the cone signals in the retina. Others, such as CIELAB, try to achieve uniformity in the sense that equal distances between stimuli in the color space go along with equal perceptual dissimilarity. What these spaces have in common is an emphasis on two separable opponent axes, sometimes corresponding to red–green and blue–yellow appearance variations and sometimes to L–M and S–(L+M) cone signals.

The organization of color in an opponent color space is in stark contrast to the way we describe colors in the real world. Color in layman's terms is almost used synonymously with hue, which is an inseparable combination of the two color-opponent axes. When we have to pick a color from a selection of different colors, it is done best by first picking the hue and then focusing on intensity and saturation [74]. Why is hue so important then in our daily lives? It turns out that hue is a major invariant property of objects, while intensity and saturation vary dramatically within objects, and even more so do cone excitations and cone-opponent stimulation vary.

We made hyperspectral measurements of 42 natural fruit and vegetable objects, resulting in complete spectral information of each pixel of the fruit images [75]. Figure 3(A) shows the fruits, and Fig. 3(B) shows the average wavelength spectrum across each individual fruit, which mainly indicates that wavelength is fairly useless in describing perceptual aspects of color stimuli. Figure 3(C) shows the distribution of colors across all objects in the a*b* plane of the CIELAB color space. While the color of a single pixel is still represented as a single point in the color space, the colors of all pixels across an object form a whole distribution in the color space, a narrow spike oriented along a single direction in the color space. The orientation of these distributions is highly constant. It is determined by the hue. The elongation reflects variance along the chroma dimension. The variability along the intensity axis is perpendicular to the plane of the color space shown here, but it can be seen in the brightness of the colored pixels. This variability in chroma and intensity is simply due to shading—the interaction of the illumination with the 3D geometry of the object. Overall, the color of an object can be fully characterized by this distribution: Hue is the orientation of this distribution in the color space, intensity is its height in the color space, and saturation is its slope in the color space. These are the three major color characteristics of each object, and they are what needs to be recovered from the visual signals entering the eye. What is also apparent from Fig. 3(C) is that in terms of intensity and saturation, the pixel distributions of the objects largely overlap in the color space, while they are uniquely characterized by their hue.

The nature of these distributions has been known for a long time [76–78]. What we argue here is that hue should be at the center of the scientific investigation of color, because it is the major invariant and diagnostic property of objects. Hue is also the property that segments different objects well. This is shown in Fig. 3(C), and another example is given in Fig. 4(A). Here, the distributions of color in the flower image of Fig. 1(C) are shown. Each type of flower or leaf occupies a separate part of the hue circle. The frequency histogram of hues in Fig. 4(C) reflects this segregation. Figure 4(B) plots the distributions in a plane of the CIELAB color space spanned by lightness (L*) and chroma (Chr*), where chroma represents the distance from the neutral gray axis. The distributions in Fig. 4(B) completely overlap in lightness and chroma, so they cannot easily be segmented using these attributes. Note that each distribution in Fig. 4(B) largely follows two line segments [shown for the purple flowers

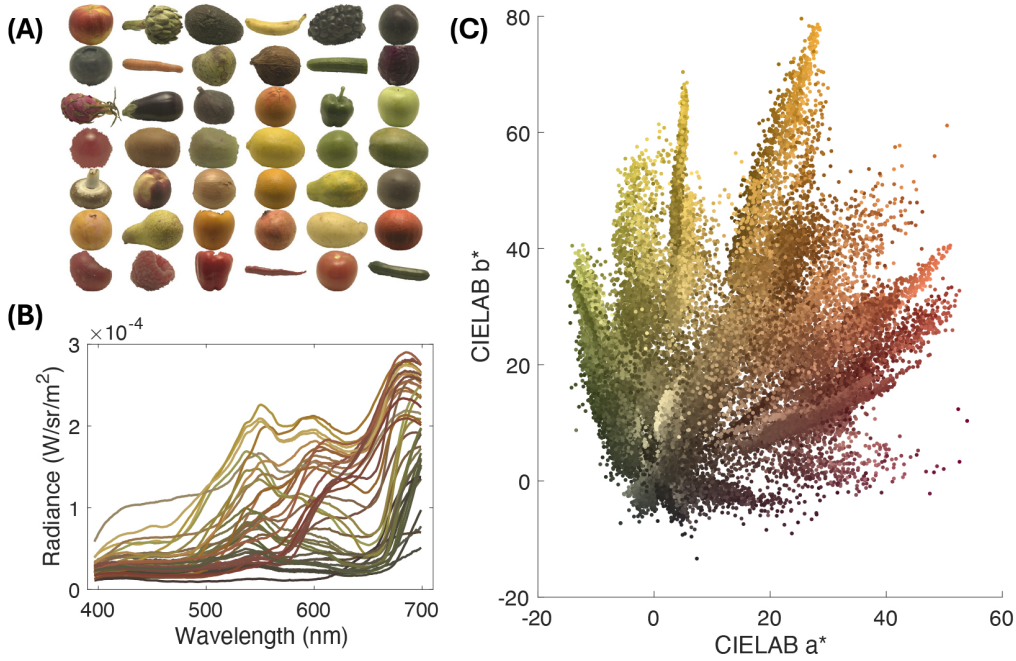

Fig. 3. Pixels versus distributions of the surface color within natural objects. (A) Hyperspectral images of fruit and vegetable objects, (B) their radiance values over the different wavelengths, and (C) their distribution in the CIELAB color space. The a*b* plane of the color space is shown, and corresponding pixels are plotted according to their L* value. Even objects with very similar colors, all falling into the same quadrant of the color space, segregate according to their hue.

in Fig. 4(B)]. One is originating at black, and chroma increases with lightness. All matte pixels fall on this line connecting black and the matte pixel with the highest lightness and chroma. The second line contains pixels to which specular reflections contribute, and chroma decreases with increasing lightness. It connects the illuminant color, which has the highest lightness and zero chroma, with the highest intensity matte pixel color. The theoretical reasoning behind these distributions was first shown for dielectric materials [79,80] and later shown to be valid for a large variety of artificial objects like plastics and paints and for natural objects like fruits and leaves [81,82].

Given the importance of hue for characterizing objects, surprisingly little emphasis has been given to hue in behavioral and physiological studies. This might have been caused partly by an obsession with so-called "unique hues," two pairs of opponent colors: red and green, blue and yellow. These pairs were thought to form a unique basis for our perception of color, in that every other color could be described as a combination of the unique hues [14,83]. When initial single-unit recordings in the retina and the LGN of monkeys observed cone-opponent responses in roughly similar color directions, it was thought that the neural basis for unique hues had been discovered and that the problem of color vision was solved. Only after careful investigation, it was realized that the retinal and geniculate cone-opponent pairs are quite distinct from the unique hues of Hering [15,16,57,84,85]. Colors along the "blue–yellow" dimension, in particular, do not appear as the colors in the Swedish flag, for example. Rather, the retinal dimension varies along the S-cone isolating direction, and lights along this dimension appear purplish (S+) or greenish–yellowish (S−). A lot of confusion has arisen out of the usage of the term "blue–yellow" for both of these color pairs, the unique hues blue and yellow, and the retinal color axes S–(L+M). This would leave the basis of the unique hues for some later, higher stage of cortical processing (see, e.g., Ref. [86]), and many attempts have been made to uncover their physiological basis (e.g., Ref. [87]; but see Ref. [88]). However, by now it seems that the very basic assumption of the theory of unique hues might not hold. The hues postulated by Hering [14] or Hurvich and Jameson [83] might simply not be unique (see Refs. [15,89–91]). This does, of course, not abolish the importance of prototypical colors and color categories, which we have reviewed in detail elsewhere [39].

With respect to hue tuning, a wide range of hue preferences was observed in visual cortex. In the retinal ganglion cells and LGN cells, preferred colors cluster around two opponent pairs of hues [21]. One of these two so-called "cardinal directions" is defined by the difference between L- and M-cone excitations, and the other one by S-cone activity only. Mechanisms for intermediate hues first emerge in primary visual cortex ([92–95]; for reviews, see Refs. [57,96,97]). A large proportion of hue-selective neurons is also found in other early visual regions, such as V2 and V3 [98,99], in mid-level visual regions such as V4 [100–107], and in higher-level IT cortex [108–111].

The chromatic properties of cells in cortical areas V1 and V2 exhibit many similarities. Approximately 50% of the cell populations in both V1 and V2 are selective for color [57,97]. Most of these color-selective cells integrate their cone inputs linearly like those in the LGN. This linear response model, initially proposed by Derrington *et al*. [21] for LGN cells, also effectively describes the responses of the majority of V1 [95] and V2 [99] cells to chromatic modulations. Despite this general trend, some V1 cells exhibit higher selectivity for color than predicted by the

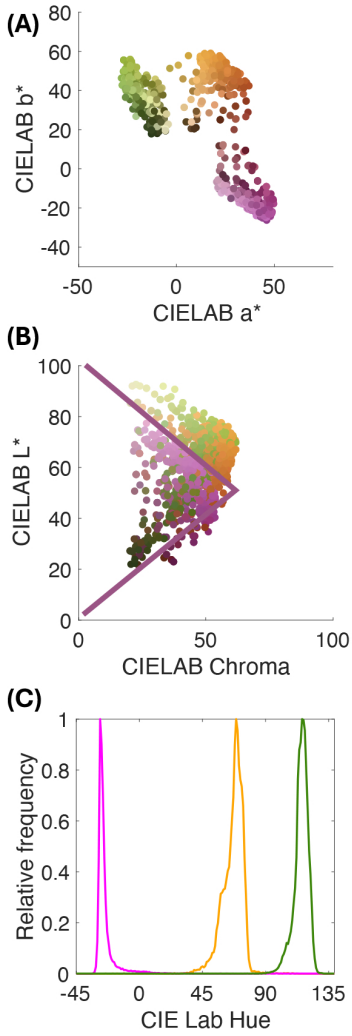

Fig. 4. (A) Pixels' distributions of colors of the flower image shown in Fig. 1(C) in an isoluminant plane of the CIELAB color space and (B) in a plane spanned by lightness (L*) and chroma (C*), the distance from the neutral gray axis. (C) Hue frequency histogram of the flower pixels.

linear model [92]. In V2, the proportion of such highly selective cells is even larger. Kiper *et al*. [99] used sinusoidal gratings with fixed luminance contrast and varying colors to assess the chromatic selectivity of V2 cells. Their findings showed that while the responses of most cells could be described by the linear model, some cells exhibited a narrower range of color responsiveness, necessitating an extended model with a nonlinear stage. This allowed computation of the bandwidth of tuning in the color space, revealing that two-thirds of V2 cells had a bandwidth close to the linear model's prediction, while the remaining third had significantly narrower tuning. Figure 5 shows two examples of V2 neurons. The cell in Fig. 5(A) responds best to yellowish–greenish hues but exhibits responses over a wide range of hues. Its tuning follows a sine wave, indicating that the response to all colors can be linearly predicted by the response to its preferred color. The cell in Fig. 5(B) responds best to reddish hues and does so in a highly selective way.

Neurons in mid- and higher-level visual cortex tend to show such narrow tuning [103,106,108,109], which allows

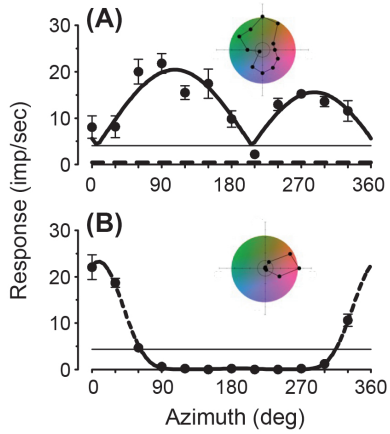

Fig. 5. Responses of two V2 neurons to drifting gratings of varying hues. The cell shown in (A) follows the predictions of a linear model (solid curve) quite closely. The neuron shown in (B) has a much narrower hue bandwidth (30 deg) and requires a nonlinear model (dashed curve). The horizontal solid lines show the cells' responses to a black-and-white grating having the same 10% luminance contrast as the colored gratings.

an exquisite decoding of hue [112]. Since many of these color-selective neurons are situated in cortical regions that are sensitive to objects such as faces, places, or food [109,113], it seems natural to assume that they are involved in the representation and recognition of these objects.

At the behavioral level, mechanisms sensitive to intermediate hues were first termed higher-order color mechanisms [114]. They have been firmly established in numerous studies using many different paradigms [115–122], making alternative explanations exceedingly unlikely [123]. Since hue is quite indicative for objects, one would also expect hue to play a dominant role in color discrimination. Interestingly, such evidence is scarce and points to a strong asymmetry in the color space. Figure 6 shows color discrimination thresholds obtained under a constant state of adaptation to a neutral gray background [27]. Each ellipse in this "clock face" represents a discrimination contour for distinguishing colors from the starred point located at its

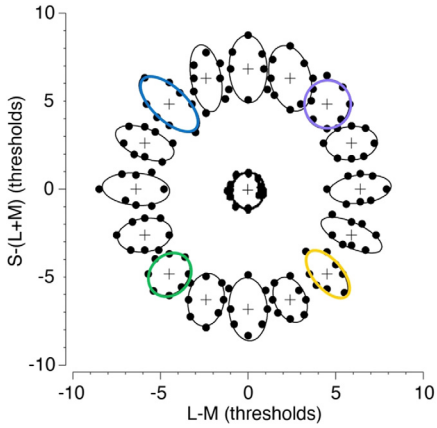

Fig. 6. Color discrimination thresholds around 16 different test locations equally spaced in the DKL-hue circle. Thresholds are normalized by the detection thresholds shown at the center. Adaptation was constant to the gray background at the center of the color space. After Krauskopf and Gegenfurtner [27].

center. Along the cardinal directions, ellipses get elongated. Thresholds get larger for increases or decreases along the same cardinal direction, while they remain constant along the other cardinal direction. This simply confirms the independence of these cardinal directions. What would one expect in intermediate directions? If only the two cardinal mechanisms would form the basis of all color discrimination, we would expect circular contours or ellipses aligned with the axes. If there would be indeed nonseparable mechanisms tuned to specific hues, then ellipses should be elongated in the direction of the specific hue.

The results show both. In the two quadrants representing orange and blue hues, the ellipses are elongated. This is mainly due to a decrease in hue thresholds accompanied by a slight increase in chroma thresholds, indicating specific tuning to these hues. However, in the other two quadrants, representing purple or green variations, the contours closely follow a circle, indicating a lack of hue tuning. This finding at first certainly seems odd, but it has been confirmed many times by now [124–128]. There seems to be an over-representation of orange and blue hues in the visual cortex [108,129–131], and it is also present in the input layers of some deep neural networks that were trained with natural images [132]. It may be related to the fact that the direction along the minor diagonal of Fig. 6 represents daylight variations [133,134], but it could also be related to an uneven distribution of colors in the world [130,135,136], similar to what is shown in Fig. 3(C).

4. COLOR AND FORM

Traditionally, form vision has been seen as primarily processing achromatic information. Edge detection in computer vision, for example, has been regarded almost exclusively in the achromatic domain (for overviews, see Refs. [137,138]). Some earlier studies on the statistics of color and luminance in natural scenes suggested that chromatic edges are often accompanied by similarly strong luminance edges [139]. We therefore analyzed the joint statistics of luminance and chromatic edges in over 700 calibrated color images from natural scenes [140]. Figure 7(A) shows an example scene from the McGill database of calibrated color images [141,142]. We decomposed the images into their luminance and L–M components and ran standard edge detection algorithms on these images. This results in a measure of edge strength at each pixel. The combined histogram of these local edge contrasts is shown in Fig. 7(B). In this histogram, the value at the position (x, y) denotes the number of pixels with edge contrast x in one channel and edge contrast y at the same location in the other channel. The darker the gray, the more frequent is the particular combination of edges. The joint edge histogram peaks at zero contrast because edges are rare events, and most pixels in an image are not an edge. This is a general property of natural images (see Refs. [143,144]; for reviews, see Refs. [145,146]).

More interesting are the points in the joint histogram that correspond to nonzero contrast in one or both channels. The histogram covers wide regions, indicating that all kinds of combinations of luminance and chromatic edge contrast occur. Some particularly interesting cases are numbered in Fig. 7. The two edges numbered 3 and 4 are pure luminance edges without any color change across the edge. They are caused by

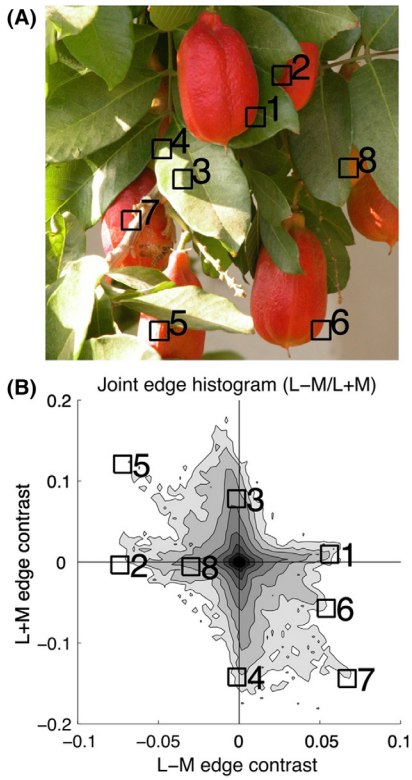

Fig. 7. Chromatic edge information. (A) An example color image showing fruits and leaves taken from the McGill database and the locations of eight different edges as discussed in the text for illustration. For edge detection, the image was decomposed into its luminance and L–M components. From the edge images, a joint edge histogram (B) is computed. The different shades of gray in the joint histogram code the different frequencies of co-occurrence of the edge contrasts: The darker, the more frequent. The joint edge histogram peaks at zero contrast, and the edge strengths in the two planes are largely independent. In the histogram, the eight edges marked in (A) are shown. After Hansen and Gegenfurtner [140].

cast shadows, and in the case of edge number 3, the shadow cuts right across a leaf. In other words, these edges are not very useful for recognizing or segmenting objects. If anything, they make the task harder. The pure color edges numbered 1 and 2 signal important object boundaries between fruits and leaves, in cases where the luminance of both objects just happens to be the same. Therefore, a larger reliance on color edges would be a useful strategy to delineate objects in the world. Overall, these pure luminance and pure color edges are rare. Most edges in natural scenes contain both luminance and chromatic information. The degree of combination varies, resulting in statistical independence between luminance and chromatic edges. These results indicate that the chromatic edge contrast is an independent source of information that can be effectively combined with other cues for accurate object segmentation in both natural and artificial vision systems. Color vision may have evolved to exploit this independent source of information in response to the statistics of natural scenes.

This result leaves open the extent to which chromatic edge contrast is actually used by the visual system to enhance object–contour perception. To explore this question, Hansen and Gegenfurtner [147] analyzed how well human-marked object

contours could be predicted using both achromatic and chromatic edge contrasts. They utilized four datasets containing a total of 824 images with human-marked contours. The images were again converted to the Derrington–Krauskopf–Lennie (DKL) color space, which separates chromatic and achromatic information in a physiologically relevant manner. Edges were detected in all three dimensions of the DKL color space (one achromatic and two chromatic). Then, these edges were compared to human-marked edge contours using receiver operating characteristic (ROC) analysis, which provides a threshold-independent evaluation. This allowed us to measure how well the luminance edges, or the color edges, or the combined edges predicted the human labels. Performance was measured by the difference in the area under the ROC curves (Δ AUC). Figure 8 shows the results for the widely used Berkeley dataset, containing 500 images with 12,000 hand-labeled segmentations of 30 human observers. Figure 8(A) shows the effect of adding color information to luminance-based segmentations. There were only two images for which the prediction became worse, and on average, the prediction advantage was around 4%. One could imagine that adding luminance information to a color-only-based segmentation would add even more predictability. However, this was clearly not the case, as shown in Fig. 8(B). Adding luminance information to color-based segmentation has, on average, no prediction advantage, which is in line with the example edges described in Fig. 7. Luminance creates many more edges, which do not directly relate to object contours and presumably play important roles for other visual functions, such as texture processing, material perception, or the perception of shadows [148–150]. These findings were confirmed [151,152] and suggest that chromatic information plays a significant role in object–contour perception.

The abundance of chromatic edges in our environment and their importance for the perception of salient object contours suggests that there should be a neuronal substrate in early visual cortex. This, of course, strongly disagrees with earlier ideas of strictly parallel visual pathways for color and form proposed by Zeki [46] and Livingstone and Hubel [44], or DeYoe and Van Essen [50]. This line of thought was based on some electrophysiological recordings showing a minority of neurons tuned to color but not to form, localized in certain cortical regions that could be identified anatomically. This would be the cytochrome-oxidase (CO)-rich blobs in V1, the thin CO stripes in V2, and area V4. At the same time, neurons tuned to form would be situated in different parts of V1 and V2 and possibly other subregions of V4.

However, this modular view has been challenged by studies showing a lack of a strong segregation of functional properties between V1 and V2 CO compartments [153–156]. For example, Gegenfurtner *et al*. [153] demonstrated that in V2, most cells are selective for both orientation and color without correlation between these properties. Similar results were found in V1 and V2 cells of awake-behaving monkeys [157] and most recently in a large 2-photon-calcium-imaging study of more than 4000 V1 neurons [93]. All of these studies perfectly agree with an initial, but mostly ignored, finding of Thorell *et al*. [40] that showed the majority of V1 neurons being responsive to luminance and color, and showing similar tuning properties for luminance and color. Similar findings were presented by Lennie

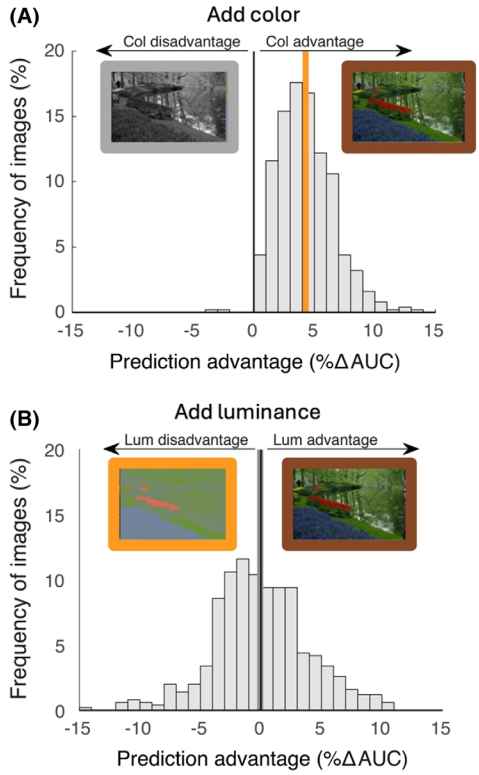

Fig. 8. Histogram of differences in area under the receiver operating characteristic curve. These are computed to assess (A) the color advantage and (B) the luminance advantage. Data are shown for the Berkeley 500 dataset and the Sobel operator. Bold vertical lines mark the average.

et al. and Johnson *et al*. [95,158], also in V1, and in extrastriate areas V2 and V3 [98,153]. These findings do not disagree with a small proportion of color cells that are only responsive to color and not tuned for orientation. However, they do fully agree with the strong sensitivity of V1 to chromatic variations that is observed in neuroimaging experiments [159–162]. This must be due to a strong response by the majority of V1 neurons that are responsive to color and luminance. Figure 9 shows an example response from a V2 neuron to sinusoidal gratings of various orientations [Fig. 9(A)] and spatial frequencies [Fig. 9(B)]. The responses to luminance and isoluminance, indicated by the black and green curves, respectively, show proportional responses and the same selectivity for near horizontal gratings of a low spatial frequency. The physiology shows very clearly that it does not make sense to divide up visual processing into luminance and a version of color processing that is confined to the isoluminant plane.

In psychophysical experiments, the major difference between achromatic and chromatic processing emerges in the contrast sensitivity function. The spatial resolution for processing achromatic stimuli generally exceeds that of chromatic stimuli, while contrast sensitivity for gratings at the lowest spatial frequencies is higher for chromatic than achromatic gratings [58–60]. This makes the spatial contrast sensitivity function band-pass for achromatic contrasts, while it is low-pass for chromatic contrasts. Despite these differences, the processing of achromatic and chromatic forms shares many similarities (for review, see

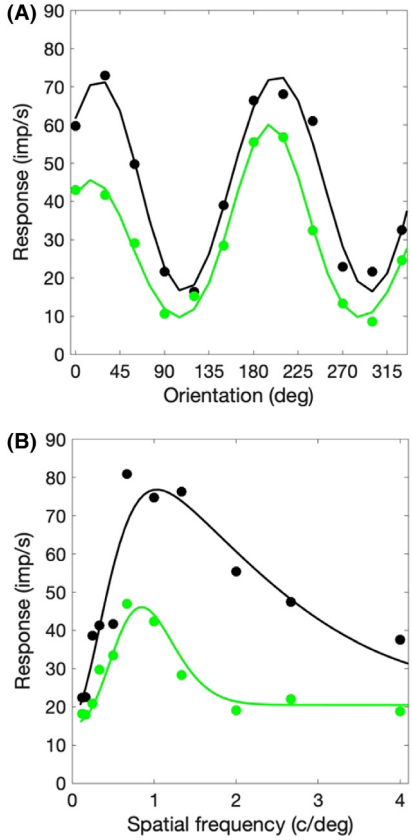

Fig. 9. Responses of a single V2 neuron to different (A) orientations and (B) spatial frequencies. Stimuli were defined by luminance (black symbols and curves) or isoluminant red–green contrast (green symbols and curves). After Kiper *et al*. [99].

Ref. [163]). Both are believed to involve multiple channels tuned to different spatial frequencies, with these channels showing similar structures for both achromatic and chromatic processing [164–168]. At higher processing stages, chromatic and achromatic processing also combine in functions such as grouping local orientations into coherent contours [169,170] and extracting object contours [171,172].

The influence of color in edge detection and shape perception is further evidenced by the persistence of visual shape illusions in purely chromatic forms. For example, in the tilt aftereffect, observers who adapt to a grating with specific stripe orientations perceive a subsequent grating as illusorily tilted away from the adapting orientation. This effect is attributed to the interaction of orientation channels that can selectively adapt, and it has been observed not only in achromatic but also in purely chromatic (isoluminant) stimuli [173]. Moreover, geometric–optical illusions, including the horizontal–vertical, Poggendorff, Ponzo, and Zöllner illusions, exhibit similar strengths in isoluminant versions as they do in their original achromatic forms [174]. These findings underscore that color information plays a substantial role in form extraction, supporting edge detection and visual shape processing even in the absence of luminance contrast.

Overall, the picture emerges that color makes significant contributions to the extraction of spatial form at low and medium spatial frequencies [175–177]. Presumably, this is the basis for its contributions to seeing things quicker and remembering them better [37,38,67].

5. COLOR CONSTANCY

The wavelength distribution entering the eye—the color signal—is the product of the spectral reflectance function of the object surface with the illuminant spectrum. The illuminant is variable and changes, for example, through the course of the day [178–180], while the reflectance function is a stable property of the surface of an object. For some of the functions of color discussed above, such as segmenting an object from other objects or the background, the illumination is less relevant, as long as there is a color difference. However, if we want to recognize an object based on its color, the effect of the illumination somehow needs to be discounted. This is called color constancy, the relative stability of color appearance of an object under different illumination contexts. Figure 10 illustrates this with two photographs of the same objects in a light box under two different illuminations, one reddish and one greenish. Despite the huge difference in illumination, the grapes appear green in both photographs, and the orange appears orange. Enlarging small parts of these two fruits in Fig. 10(B) indicates just how much the color coordinates of these patches change when changing illumination. It also illustrates that the pixel color distribution of the orange under the greenish illuminant and the grape under the reddish illuminant is very similar. How does the visual system deal with such massive changes in its input to achieve color constancy? Can it achieve color constancy?

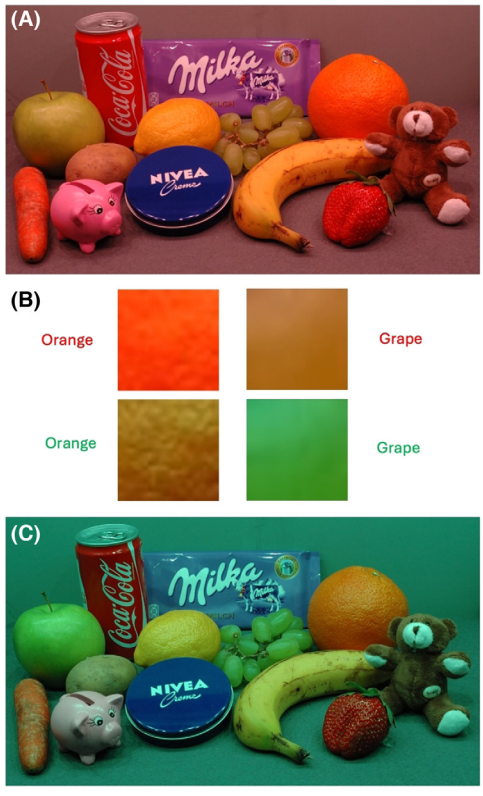

Fig. 10. Illustration of color constancy. A scene with several objects was photographed in a light box under (A) reddish and (C) greenish illuminations. (B) Enlarged image regions of the orange and the grapes under these two illuminations.

Laboratory measurements of color constancy have yielded highly variable results, ranging from minimal to nearly perfect constancy (for reviews, see Refs. [39,181]). Zero constancy would mean color matches under different illuminations are based solely on cone excitations without illumination adjustment. Conversely, 100% constancy would indicate matches based on the same physical object under different illuminations. These extremes define a color constancy index that quantifies how close a match is to either extreme [181]. Figure 10 illustrates that viewing two images side by side leads to constancy indices somewhere in between 0 and 1. If constancy were perfect, the appearance, for example, of the grapes or the orange in the top and bottom images would be identical. This is not the case. We can tell that the orange is more reddish and more intensely colored in the top image, under the reddish illumination. The grapes appear to be a more saturated green in the bottom image, under the greenish illumination to the right. However, the fruits also appear different in the context of the image, compared to their isolated views in the center, which would correspond to the zero constancy case. This intermediate level of constancy is typical for situations when the two illumination contexts are given side by side at the same time, as was the case in many of the early quantitative experiments (e.g., Ref. [182]).

The observers simply cannot adapt to both scenes at once. Chromatic adaptation significantly impacts constancy. While some adaptation occurs within fractions of a second, full adaptation can take several minutes [183]. Methods such as successive surface comparisons, achromatic adjustment, and categorization across illuminants facilitate high levels of adaptation. However, measurements may vary depending on factors like memory limitations in successive constancy [78], categorization differences among observers and colors [184,185], or the presence of achromatic cues [186]. Studies have shown that under certain conditions, observers can achieve near-perfect color constancy (90% or above) when adaptation is ensured [78,184,185,187–189] or when using naturalistic scenes with many cues available [187,190]. Notably, there is a trend toward higher constancy indices in more recent studies, possibly due to the increased use of naturalistic environments and tasks [39,191,192].

It should also be noted that color constancy, like other perceptual constancies, is a mathematically underdetermined problem that, strictly speaking, cannot be solved. Indeed, color constancy does not work under all conditions; surfaces and illuminants must have specific spectral properties. For instance, clothing viewed under poor artificial lighting in a store may look different under daylight. This demonstrates metamerism—surfaces that match in color under one illuminant but differ under another [193–195]. Metamerism does occur in the natural world, but whether this is considered frequent or rare is a matter of debate and interpretation [196–200]. From the above discussion of the natural variation of lightness and chroma within objects, it follows that metamerism should probably be treated in an object-defined manner, rather than pixel-wise. Overall, our human visual system seems to be well-adapted to environmental conditions [136,201], in order to achieve high color constancy for most real objects and materials under natural lighting.

The different computations employed by the visual system to achieve color constancy have been studied extensively [181,202]. The degree of color constancy can range from near zero to almost perfect based on the presence of different cues [188,203]. Three main mechanisms by which color constancy is achieved were identified. The color contrast across local edges, such as between an object and its background, remains relatively consistent despite changes in illumination [204–207]. The region of maximum flux often corresponds to a white object and can be used as a reference point (the "brightest is white" principle; [208–211]). The average color of a scene is often close to a neutral gray (the "gray world" hypothesis), which proposes that we adapt to the average color within a scene, perceiving it as gray [212,213]. These mechanisms highlight how our visual system maintains color consistency across varying lighting conditions. Additionally, color constancy may involve comparing colors to other references or anchors. This inferential constancy is influenced by factors such as three-dimensional interreflections and shading [214], depth segmentation [215–217], specularities [218–223], and memory colors ([224,225]; but see Ref. [226]). In summary, the variability in color constancy measurements is understandable when considering the spectral properties of surfaces and illuminants used as stimuli and the presence of cues for adaptation, simultaneous contrast, and anchoring. Most everyday situations likely involve full-field adaptation, local contrast, and scenes with many color cues, suggesting that color constancy in natural situations should be at least as high as under optimal experimental settings.

While it is very reassuring to have high color constancy in the real world, the real world is very difficult to experiment with. Experimental manipulations are cumbersome and might involve changing the back wall of an experimental chamber [203] or replacing color filters on the windows [227]. Fortunately, there have been massive advances in virtual reality (VR) in recent years that allow photorealistic rendering of indoor and outdoor environments. We have recently shown that VR headsets can be characterized and calibrated quite well [228,229]. We have used these procedures to evaluate color constancy in such rendered environments [230]. Our results are highly promising. In agreement with earlier studies in natural environments, we found very high levels of color constancy when all cues were present in the scene. The degree of constancy was attenuated when cues were removed from the scene. This could easily be achieved, for example, by putting the test objects, in our case lizards, on surrounds (the rose-colored leaves) whose chromaticity was held constant across illumination changes (Fig. 11). Without the local surround cue, color constancy decreased, but the decrease was dependent on the illumination change. It was largest for the change to a greenish illumination, which in color space lies in the opposite direction to the pinkish context of the leaves. We confirmed this systematic effect in newer experiments where we tested all combinations of surrounds and illumination changes (see Ref. [231]).

Interestingly, the effect of removing the average color cue depended on how this was implemented. Figure 12(A) shows our indoor scene under a neutral illumination. In Fig. 12(B), the same scene is illuminated by a yellowish light. The average chromaticity of the scene shifts toward yellow. How can we have such an illumination shift without changing the average color? One possibility, shown in Fig. 12(C), is to shift the reflectance

Fig. 11. 3D-rendered indoor scene under (A) neutral and (B) yellowish illuminations. The local context cue is eliminated by presenting the test objects (lizards) on rose-colored leaves that keep the same chromaticity under both illuminants.

of each object in the scene in the direction opposite of the illumination change. The gray-looking chair needs a bluish tint so that it can stay gray under the yellowish illuminant. Of course, the net effect of this, when applied to each surface, is a scene that is exceedingly difficult to distinguish from the one in Fig. 12(A). Previous work by Gilchrist and Ramachandran [232] has indeed shown that only interreflections and specular reflections can be used to tell the two combinations of illumination and object reflectance apart. In our experiments, the color constancy index fell to values near zero in this case. In Fig. 12(D), another way is shown to keep average color constant throughout an illumination change. Here, we added new objects all over the scene that would balance the change in average color. We made sure that this was the case independently of where the observers fixated. When doing so, color constancy still decreases, but the decrease is only to about 50% of its original value. The computations underlying color constancy do not happen in a relatively "naive" pixel-by-pixel approach. Rather, it seems that the scene is first segmented into different objects and a background.

Given that the mechanisms by which the human visual system achieves color constancy are quite well studied by now, it should not come as a surprise that theoretical and computational approaches to solve the problem are also well established and fairly advanced (for summaries, see Refs. [202,219,233,234]). The proposed algorithms are straightforward and can be readily applied to input images. The output of such algorithms is often a white-balanced version of the input image, simulating its appearance under a neutral illumination. It can also be an estimate of the illumination, which can then be used to color-correct the input image. Given the overall success of these computations [235–239], it is actually surprising to see that work on computational algorithms for color constancy has not subsided. Quite the opposite, the overwhelmingly successful introduction of deep neural networks into vision science in 2012 [240] has led to numerous approaches applying DNNs to color science [241–243].

There are several advantages to using DNNs. Large networks that were extensively trained for object recognition can be evaluated in terms of their color processing. We and others have, for example, observed that object-trained DNNs exhibit similarities to the human visual system's processing of color [132,244–247]. In another study, we have shown that a DNN trained on object recognition exhibits relatively stable color categories when tested in tasks that were previously used in animal learning [248]. The major advantage is that many of these networks can simply be used to implement specific tasks akin to human psychophysics [249–251]. Color constancy is a bit more tricky since the images used for training are typically white-balanced already. Therefore, object recognition networks

Fig. 12. Indoor scene under (A) neutral and (B) yellowish illuminations. In panel (C), the change in average color is balanced by changing the reflectance of each individual object in the direction opposite of the illumination change. In panel (D), the same is achieved by adding new objects such as the plants and the pictures.

only learn a single, neutral illumination and thus should not be able to learn color constancy. Accordingly, such networks perform poorly when tested with images taken under chromatically biased illuminations [132,252]. This can only be resolved by acquiring large datasets with ground truth measurements to extend the training of these networks to different illumination conditions. However, this is easier said than done. Large hyperspectral datasets with reflectance information are rare, and even color-calibrated RGB images are not widely available (e.g., Refs. [241–243]).

We have used computer graphics-generated scenes as a way to circumvent the ground truth issue [252,253]. Using hyperspectral rendering, the surface reflectance and the illumination spectra can be fully determined. We have used the Munsell chip reflectance spectra covering the whole of color space [254] and measurements of natural illumination spectra [178,255,256], together with the Mitsuba physics-based rendering engine, to create relatively simple scenes. The advantage is that we can specify the ground truth at every pixel and that we also have information about which pixels belong to which object in the scene. In a first attempt, we devised a modestly deep network to recover the reflectance of a single object in a scene [253]. The network established a representation of color in terms of hue, saturation, and lightness, and its performance under various cue conditions at least qualitatively mimicked human observers. We improved upon this by building a more elaborate network that aimed to recover the spectral reflectance of each individual pixel in a scene with multiple objects. The overall error was modest and on the order that humans would make. It could be decomposed into errors within objects, giving variable estimates of the object's reflectance, and errors where the average estimate for an object deviated from the ground truth. Unfortunately, models trained with relatively simple computer graphics scenes do not readily generalize to more complex natural scenes, especially outdoor scenes. We are currently trying to evaluate network performance with the photorealistic environments we used in the VR experiments. For these scenes, we not only have rich ground-truth information, but also a vast amount of data from human observers.

6. SUMMARY

Color vision is not merely about detecting pixel-level differences or reproducing exact images but about enabling us to navigate and interact with the natural world by recognizing and distinguishing objects. This review presents an integrated perspective on color vision, emphasizing its role in object recognition and segmentation. Moving beyond traditional views of independent processing of color and form, it is shown how color contributes significantly to spatial vision and object memory. Central to this understanding is the concept of hue as the most invariant and diagnostic property of objects, as shown through hyperspectral analyses and behavioral experiments. Furthermore, color constancy emerges as a critical function, allowing stable object recognition under varying illuminations. Of central importance to this approach is the study of color vision under highly controlled conditions using natural stimuli. All the tools are readily available at this time. Advances in hyperspectral imaging techniques allow the acquisition of complete natural environments [257,258], computer graphics enable us to create hyperspectral virtual environments of great complexity, which we can display in fully calibrated VR headsets, and all of these stimuli can be used in deep learning frameworks to achieve computational solutions for machine vision and to perform deep psychophysics to model human vision.

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