Opinion

Color appearance and the end of Hering's Opponent-Colors Theory

Bevil R. Conway , [1,*] Saima Malik-Moraleda, [2,3] and Edward Gibson [2]

Hering's Opponent-Colors Theory has been central to understanding color appearance for 150 years. It aims to explain the phenomenology of colors with two linked propositions. First, a psychological hypothesis stipulates that any color is described necessarily and sufficiently by the extent to which it appears reddish-versus-greenish, bluish-versus-yellowish, and blackish-versus-whitish. Second, a physiological hypothesis stipulates that these perceptual mechanisms are encoded by three innate brain mechanisms. We review the evidence and conclude that neither side of the linking proposition is accurate: the theory is wrong. We sketch out an alternative, Utility-Based Coding, by which the known retinal cone-opponent mechanisms represent optimal encoding of spectral information given competing selective pressure to extract high-acuity spatial information; and phenomenological color categories represent an adaptive, efficient, output of the brain governed by behavioral demands.

The brain basis for color appearance

The color of the year is Viva Magenta, 'a pulsating color whose exuberance promotes a joyous and optimistic celebration';[i] or Spanish Moss, 'a midnight green that has a strong connection with the richness of nature';[ii] or Raspberry Blush, 'a vibrant orange–red shade that instantly brings joy to your home'.[iii] The kaleidoscope of options illustrates the importance of color, while the baroque names underscore a peculiar paradox. Each color can be specified by three numbers – the activity of the three cone types – but this trichromatic code does not capture color appearance. The same code can appear to be very different colors, depending on context and expectation, as illustrated by #thedress [1].

In the 19th century, Ewald Hering proposed an alternative to trichromacy as the explanation for color appearance [2]. His Opponent-Colors Theory (Figure 1) seeks to explain what colors look like with two propositions. First, a perceptual hypothesis invoking a specific instantiation of **color opponency** (see Glossary) which stipulates that any color can necessarily and sufficiently be described by the extent to which it appears reddish-versus-greenish, bluish-versus-yellowish, and blackish-versus-whitish; the six colors defining Hering's theory came to be called **unique hues**. Second, a physiological hypothesis which stipulates that the perceptual mechanisms are coded by three innate and discrete neurobiological processes. The theory is a showcase **linking proposition** in cognitive science [3].

Shortfalls of the theory notwithstanding [4–11], it remains an accepted view. On the perceptual side of the linking proposition, the expert's handbook defines hue as that 'attribute of visual perception according to which an area appears to be similar to one of the colors, red, yellow, green, and blue' [12]. Commercial color systems are defined by Hering's opponent-color pairs [13,14]. And textbooks state that color appearance is arranged around 'four basic [unique] colors in two opponent pairs: red versus green, and blue versus yellow' [15]. On the physiological side of the linking

Highlights

The essay reviews the psychological and physiological evidence for Opponent-Colors Theory and concludes the theory is wrong.

Behavioral work shows that the theory's three appearance mechanisms (red-versus-green, blue-versus-yellow, and black-versus-white) are not necessary to describe color.

Physiological work shows that neural color-encoding mechanisms are not characterized by tuning to the opponent colors of the theory. Contrary to Opponent-Colors Theory, the color-encoding mechanisms of the brain are not evident in perception.

A new Utility-Based Coding framework is described, by which color depends on many interacting brain areas. Encoding mechanisms efficiently capture and transmit to the cortex as much chromatic information as possible given selective pressures for both color and high acuity vision, while appearance reflects adaptable neural operations that optimally support behavior under changing contexts and objectives.
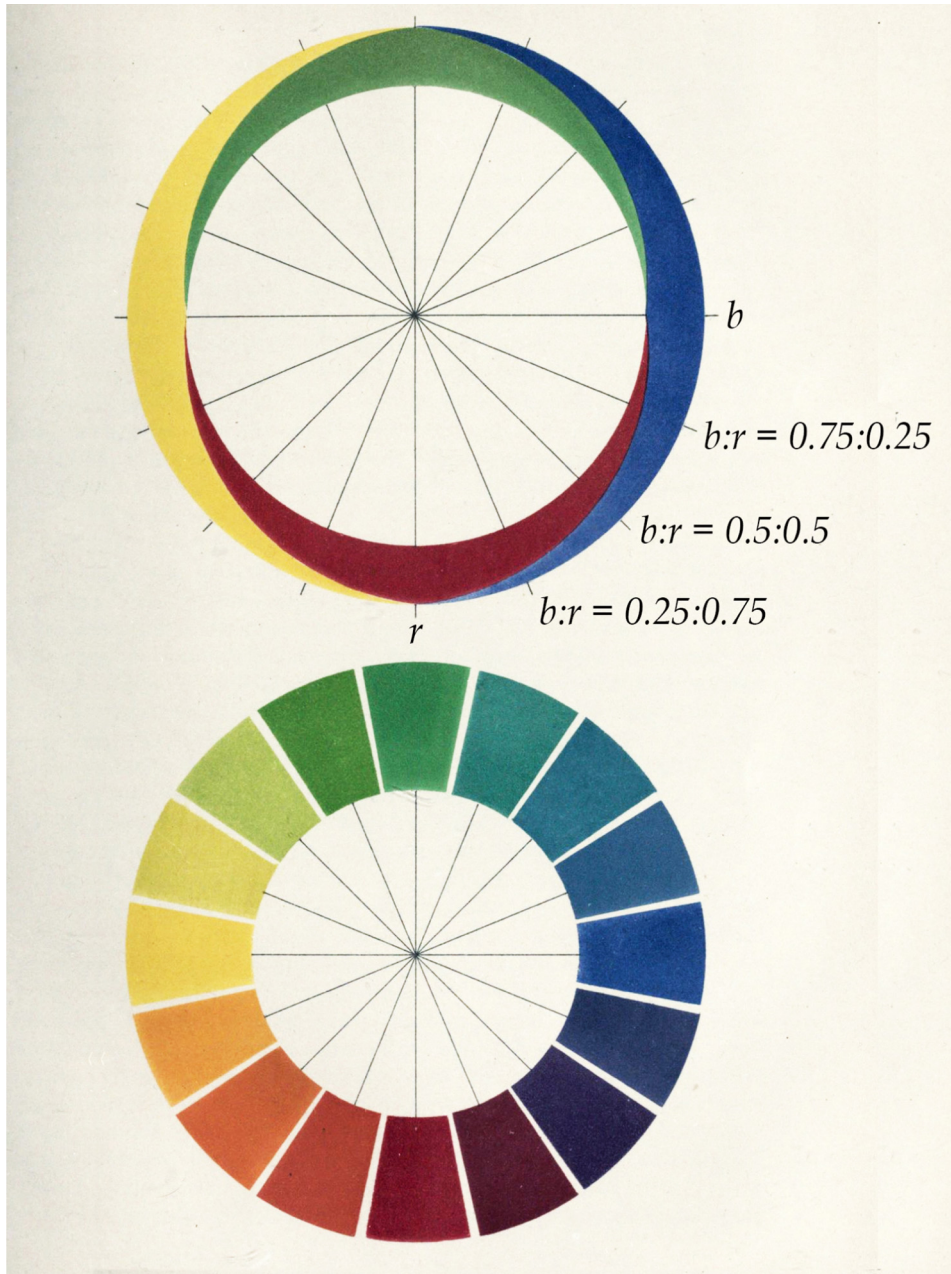
[1]Laboratory of Sensorimotor Research, National Eye Institute and National Institute of Mental Health, Bethesda, MD 20892, USA
[2]Department of Brain and Cognitive Sciences, M.I.T., Cambridge, MA 02139, USA
[3]Program in Speech and Hearing Bioscience and Technology, Harvard University, Cambridge, MA 02114, USA

*Correspondence:
bevil@nih.gov (B.R. Conway).

Trends in Cognitive Sciences

Figure 1. Hering's Opponent-Colors Theory. Diagram by Ewald Hering illustrating Opponent-Colors Theory. According to Hering, 'the six basic sensations of the visual substance are arranged in three pairs: black versus white, blue versus yellow, green versus red. Each of these three pairs corresponds to a distinct process of dissimilation and assimilation, such that the visual substance can undergo chemical or metabolic change in three different ways' (p. 118 in [2]). In the top panel, 'r' is red, 'b' is blue, and the ratios indicate the combinations of these components in each color mixture of the bottom panel. So, purple has a ratio of blue to red (b:r) of 0.5:0.5. Hering's theory boils down to two ideas: (i) that the appearance of any color is necessarily and sufficiently described by the extent to which it is reddish-versus-greenish, bluish-versus-yellowish, and blackish-versus-whitish; and (ii) that these appearance mechanisms are hardwired in the nervous system.

Glossary

Color afterimage: the color seen after adapting to a colored display. The afterimage of red is bluish green.

Color-matching experiment: a test projected in one half of an aperture is matched by adjusting the intensities of three primary lights projecting to the other half of the aperture. There is a unique solution for all tests. The three primaries can have any spectral composition, so long as each cannot be matched by a combination of the other two. Results with one set of primaries can be linearly transformed to predict results obtained with other primaries. The intensity values of the three primaries needed to match each wavelength across the visible spectrum comprise color matching functions.

Color opponency: a perceptual phenomenon whereby two colors are mutually exclusive. Hering's Opponent Colors Theory specifies three pairs of opponent colors as necessary and sufficient for describing the appearance of all colors: red-versus-green; blue-versus-yellow; and black-versus-white.

Complementary color: the light that when added to a test renders the test colorless. Every color has a complementary color, roughly opposite in the color circle, so there are almost an infinite number of complementary colors. The existence of complementary-color pairs is evidence that the visual system encodes colors with some form of opponency.

Cone: a type of retinal photoreceptor. There are three types of cones, called L, M, and S, for their peak wavelength sensitivity to long, middle, and short wavelengths. The spectral tuning of L, M, and S cone cells overlap extensivity; the L and the M cone cells have about 98% overlap.

Cone opponency: a physiological operation implemented by retinal bipolar cells that recovers spectral information by pitting excitation by one cone class against inhibition by another cone class.

Hue-cancelation experiment: an observer is asked to adjust a red, green, blue, or yellow light to cancel the appearance of green, red, yellow, or blue in a test. For an orange test, a participant would add enough green to cancel the reddish quality; the result defines unique yellow. These experiments were taken as evidence for Hering's Opponent-Colors Theory, but a theory that red, green, blue, and yellow are privileged

proposition, contemporary neurophysiological studies are often guided by Hering's theory [16–19]. Here, we review the evidence on each side of the linking proposition and argue that the theory does not need modification, it needs to be discarded. We then sketch out an alternative.

Hering's Opponent-Colors Theory

Two intuitions dating to pre-Socratic philosophers are that existence depends on the unity of opposites (love/strife; hot/cold; light/dark, etc.), and that some colors are elementary. The number of elementary colors has never been settled. Empedocles and Aristotle identified two (white and black). Leonardo DaVinci declared that Nature produces eight colors, but he said that 'Blue and green are not simple colours … for blue is composed of light and darkness [and]…green is composed of a simple and a mixed colour' [20], p. 98). Peter Paul Reubens argued for three. Isaac Newton thought there were five and then revised to seven. Johann Wolfgang Goethe recognized six. Hering entered the fray in the 1870s, penning his theory uncoincidentally in the same year that his countryman Wilhelm Kühne coined the term enzyme. Hering's theory married the two ancient intuitions and consecrated the union with a mechanistic hypothesis borrowed from the new field of physiological chemistry: there are four chromatic colors, and each derives its special status as the unopposed product of a biochemical process. Hering had no data. Rather, he used introspection to formulate, mathematically, his experience (Figure 1), surmising that each color-opponent experience 'corresponds to a distinct process of dissimilation and assimilation' of a 'visual substance' ([2], p. 74). Hering's hypothesis was compelling, for it not only invoked Johannes Müller's idea of 'specific nerve energies' but also gave scientific muscle to Goethe's poetic descriptions of **color afterimages**, which imply that opponency of some form must underwrite color appearance.

In the 20th century, Hering's theory came to mean 'the coding of color experience at the neural level' by 'the simplest linkage between receptor events and neural events' ([21] pp. 128–136). In the 1950s, proof seemed in hand. **Hue-cancelation experiments** were taken as support for the first proposition [21]. And neurophysiological recordings in macaque monkeys, obtained at the same time and institution [22], were considered evidence of the second proposition. In Horace Barlow's words, 'a startling confirmation of Hering's long-standing hypothesis about the reciprocal organization of colour systems' [23] (neural excitation/inhibition substituted for biochemical assimilation/dissimilation). The combination of behavioral and neurophysiological data 'catapulted opponent-colors theory from a special-purpose model, known only to color specialists, to a central idea in vision science' ([24], p. 319).

The historical importance of Hering's theory is hard to overstate. It signaled a shift in the search for causal explanations of color from the physical (spectrum) to the physiological (eye/brain) that motivated the first neurophysiological studies of color [25,26]. One long-recognized problem, though, is that those studies and all others since do not provide data that clearly line up with Hering's opponent colors. Experts today, therefore, think the theory is inaccurate, but they nonetheless think it accounts for something essential. To sort through the muddle, we need to maintain the distinction between **trichromacy**, Hering's Opponent Colors (the unique hues), Hering's theory (the linking proposition), and general concepts of color opponency and **cone opponency**. Opponent-Colors Theory neither contests nor establishes trichromacy, proven by the **color-matching experiments** of James Clerk Maxwell [27] and implemented by the three classes of **cones** [28]. Hering's theory is also independent of the idea that color depends on some form of opponency. As Maxwell pointed out, the brain must compare photoreceptor signals, by subtraction or ratio, to achieve color appearance. Proof of color opponency was established decades before Hering, with the discovery of **complementary-color** pairs and color afterimages [29,30]; color opponency is implemented by retinal cone-opponent neurons [22]. Trichromacy and complementarity organize colorimetric space [31], and Hering's theory can be discarded without threatening these well-established principles.

cannot be tested with an experiment where these are fixed parameters.
Linking proposition: a hypothesis that aims to explain a psychological phenomenon by a direct link to physiological processes; also known as a linking hypothesis.
**Trichromacy:** the idea that color is coded by three variables.
Unique hues: the six Urfarben ('source colors') defined by Hering's Opponent-Colors Theory, deemed psychologically pure: red, green, blue, yellow, black, and white. The Theory states that each unique hue cannot be described by any other term, and all colors can be described by combinations of unique hues.

Lack of neurophysiological evidence for Hering's Opponent-Colors Theory

Neurons in the lateral geniculate nucleus (LGN) of macaque monkeys, a model of the human, show overt spectral opponency: their firing rates increase or decrease depending on stimulus wavelength [22]. These cells were christened 'red excitatory and green inhibitory', or 'blue excitatory and yellow inhibitory' to endorse the view that they are the substrate for Hering's theory [32]. But despite the nomenclature, the colors that maximally modulate LGN cells are not Hering's opponent colors (Figure 2B) [33]. For example, so-called 'blue–yellow' cells respond best to lavender and lime [34], colors that strongly modulate S cones. Neurophysiologists continue to discover varieties of cone-opponent neurons, often describing them with Hering's opponent-color terms [35,36], a 'quirk of nomenclature' [9] that demonstrates Hering's grip.
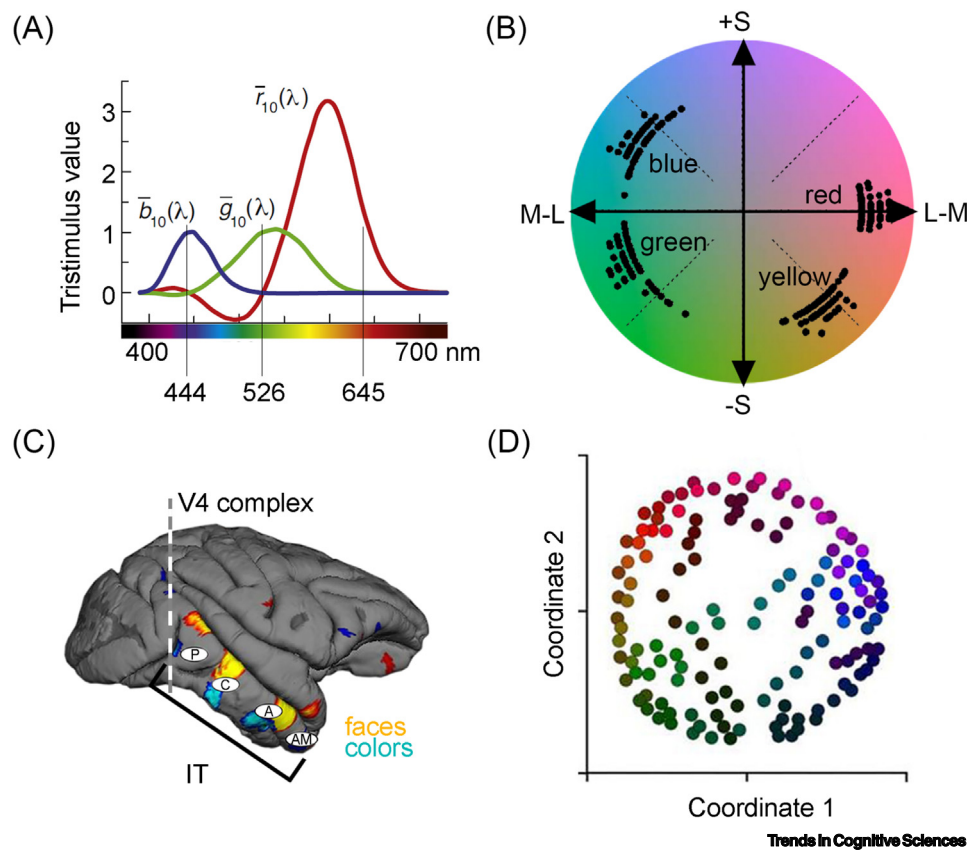
Figure 2. Color encoding and neural representation. (A) Color matching functions for targets that are 10° in diameter [28]. The y axis shows the value of each of three primary lights (444, 526, and 645 nm) required to match each monochromatic test light on the x axis. To match some test lights, the primary must be added to the test not to the other primaries, indicated by negative numbers. Color-matching data provide evidence of the essential trichromacy of human color vision. (B) Distribution of unique hue settings for 51 observers projected onto a cone-opponent color space [33]. The axes isolate the two cone-opponent mechanisms of the retina; colors along the x axis vary only in their L and M modulation; colors along the y axis vary only in modulation of the S cone. (C) Lateral view of the macaque brain showing functional domains biased for colors and faces, identified in 'high-level' visual cortex with functional MRI. The vertical line shows the plane of section of the V4 complex. The white ovals indicate four stages in inferior temporal cortex defined by functional and anatomical data (P, posterior; C, central; A, anterior; AM anterior–medial) [55,59]. The existence of color-biased domains in inferior temporal cortex implies that color depends on high-level perceptual and cognitive operations. (D) Geometry of the neural representation of color for neurons within the color-responsive subcompartments of the V4 Complex, calculated by multidimensional scaling [57]. Stimuli are plotted by the 2D embedding determined by the responses of 300 cells.

Can we keep Hering's theory afloat by dismissing as trivial the mismatch in color tuning of cone-opponent cells and Hering's opponent colors? No, we cannot. Hering's theory was important precisely because it directly linked color appearance with physiological mechanisms, so the mismatch is fatal to the theory. In fact, contrary to Hering's theory, the visual system seems set up to overwrite any privilege in the perception of colors associated with cone-opponent mechanisms, for there are few suprathreshold color-appearance phenomena distinguished by the colors that best modulate the mechanisms.

Perhaps Hering's theory finds its implementation in V1, the target of the LGN? Many studies have measured V1 responses, and many mysteries remain. But one thing is clear: V1 responses do not line up with Hering's opponent colors [37–43], not even for the cells with overt chromatic opponency [44]. Yet V1 responses, like retinal cone-opponent responses, are still often characterized using Hering's theory [19].

Is Hering's theory implemented downstream of V1? Neurons that respond to color are found in many brain regions, including V2 [45–48], the V4 complex [49–52], inferior temporal cortex [53–55], and frontal cortex [56] (Figure 2C). Color-responsive cells throughout these regions typically do not show overt color opponency, but perhaps they serve Hering's theory through a bias for unique hues? Here, again, the answer is no. We initially thought that color-responsive cells in V4 represent unique hues [16], but this conclusion was a mistake that reflects a confound of saturation and hue [57]. When unconfounded, the population shows a relatively uniform representation of colors (Figure 2D). Meanwhile, inferior temporal cortex, the culmination of object vision, reflects the color statistics of objects, which are also not aligned with unique hues [58]. Only one study has found neural evidence that unique hues are privileged [17]. That evidence reflects activity far beyond perceptual encoding and is therefore irrelevant to Hering's theory.

The neurophysiology shows that the biological side of Hering's theory is wrong. Color engages surprisingly vast cortical resources [59], which implies that color appearance is not accomplished with so simple a mechanism as Hering imagined. So, what about the other side of Hering's linking proposition?

Hering's original argument

Hering put forward two arguments. First, that mixtures of his opponent colors ('reddish green') are inconceivable. This may be true, but it is not compelling. There are an infinite number of inconceivable mixtures, including mixtures of all complementary pairs, e.g., 'greenish magenta', 'cyanish pink', 'orangish cobalt', and 'indigoish yellow'. Second, Hering argued that unique hues are unique insofar as they describe all colors and cannot themselves be described. Yet many colors are arguably not adequately described as mixtures of unique hues. Is the saturated peel of an orange really 'reddish yellow'? Or is orange unique? What about purple?

Early debates went in circles struggling to reconcile Opponent-Colors Theory with Maxwell's trichromacy. A way forward was provided by 'zone theories' [60,61], which implement Hering's opponency immediately downstream of the cones. The approach required a bit of math to relate the cones' wavelength sensitivity with Hering's 'valence' curves (see Figure I in Box 1). Erwin Schrödinger (the physicist with the imaginary cat) conjured the math [62], relying on Hering's logic that all colors can be described by linear combinations of unique hues (Figure 1). The synthesis yielded many testable predictions. Hering's theory has failed almost all of them (Box 1). So, is there any behavioral evidence for the theory?

Box 1. Hering's Opponent-Colors Theory fails many psychophysical tests

Objective tests of Opponent-Colors Theory became possible when the theory was formulated as a hypothesis about how cone signals are transmitted to perception. The formal exposition spells out the mathematical transformation of cone responses to opponent-color pairs [132] (Figure I); baked into the math is the linearity of Opponent-Colors Theory implied by the description of color appearances as simple (mathematical) combinations of red-versus-green, yellow-versus-blue, and black-versus-white (see Figure 1 in main text).

Many psychophysical experiments have tested whether judgments of the redness-versus-greenness, blueness-versus-yellowness, and blackness-versus-whiteness of colors is predicted by the linear readout of cone (or cone-opponent) responses. One prediction is that in any color space, the line connecting unique red and unique green, and the line connecting unique blue and unique yellow, should intersect at the achromatic point in the space. This prediction fails: neither of these lines pass through the achromatic point; their intersection is yellowish and the line connecting blue and yellow passes through pink, not white [27]. Considerable work has confirmed the nonlinear relationship of cone responses to color appearance [133–136]. Moreover, the extent to which a light partakes of a unique hue sensation varies with the energy level of the light (the Bezold–Brücke phenomenon; [137]) and with its saturation (the Abney effect; [134]), which further confirms that the Hering opponent mechanisms do not correspond to linear combinations of the cones. In addition, the color appearance associated with an increase in S-cone activity can be blue or yellow depending on the activity of the L and M cones, which would imply that blue–yellow judgements are not only nonlinear but also nonmonotonic [136,138]. In other psychophysical tests of the theory, Mollon and Cavonius measured wavelength discriminations around unique yellow following low-intensity adaptation to monochromatic lights. They found that discriminations of wavelengths around unique yellow were different following adaptation to short wavelength (blue) light compared to middle wavelength (yellow) light, which violates Opponent-Colors Theory since discriminations of unique yellow should only be impacted when adapted to lights that appear reddish or greenish [139]. Finally, psychophysical studies have tested the predicted number of color-opponent mechanisms and the independence of the color opponent and luminance-opponent mechanisms; these studies have found more color channels than predicted by Hering's theory [103,140,141] and interactions among the channels that violate Hering's theory [142,143].
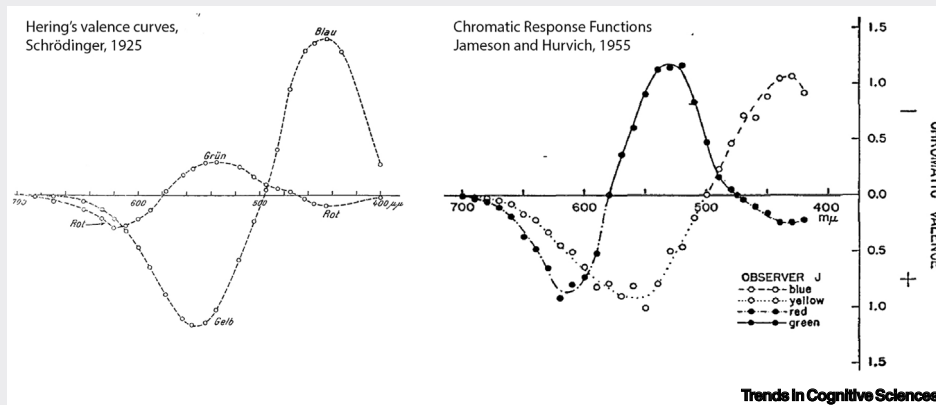

Figure I. Hering's valence curves (left) and Hurvich and Jameson's hue-cancelation curves (right). The y-axis scaling is arbitrary. Both curves plot the amount of redness, greenness, blueness, and yellowness associated with each wavelength, and show the same pattern of results (note the location of the curve crossings; grün, green; rot, red; blau, blue; gelb, yellow). The valence curves were derived on introspection; the hue-cancelation curves were based on hue-cancelation experiments.

Hue cancelation

Classic hue-cancelation experiments remain the primary evidence. The data are quantitative, but the evidence they provide turns out to be no stronger than that offered by Hering's intuition [5]. Indeed, hue-cancelation curves are identical to Hering's valence curves, which were obtained without running any experiments at all (see Figure I in Box 1). The difficulty is that both sets of curves beg the question they are ostensibly trying to answer [63]. They are what you get if you privilege red, green, blue, and yellow, not a test of the privilege of these colors. They test sufficiency not necessity.

If unique hues are truly privileged, then it should be unimaginable for participants to rate the proportion of teal, purple, orange, and lime in test colors that are uniquely 'red', 'yellow', 'green', and 'blue'. Philosophers had assumed this was unimaginable [64], but surprisingly participants are perfectly capable of seeing mixtures of intermediate colors within unique hues (Figure 3A) [63]. Other work confirms that the best criteria for demarcating unique hues also demarcate secondary colors [65]. The formal distinction between unique and secondary colors has fallen away.

To reject Hering's theory one might ask for studies showing that participants can adjust the proportion of lime to neutralize the appearance of purple in a test. If so, is the result unique orange? This would be analogous to the case where the green needed to neutralize the red in an orange test is a probe of unique yellow. But such measurements are unnecessary to reject Hering's theory, given that people's 'unique' settings change depending on the prompt. Settings for unique yellow are different if asked to pick a color that is 'neither greenish nor reddish', 'neither tealish nor reddish', or 'neither greenish nor purplish' [63]. Such task dependence is incompatible with Hering's theory of hardwired encoding.

Hue cancelation in nonwestern cultures

The generalizability of Hering's theory has been tested in other cultures. The Tsimane' of the Amazon jungle have a word corresponding to 'red' but no consistent term for 'yellow'. 'Green' and 'blue' are
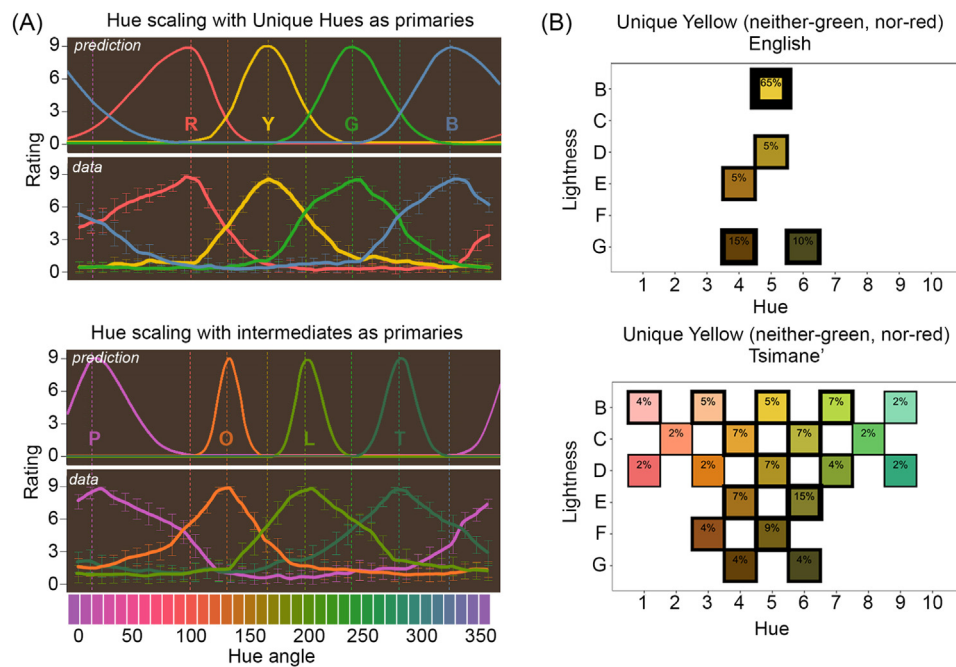
Figure 3. Purple, orange, lime, and teal can be used as perceptual primaries akin to unique hues. (A) Hue scaling in which participants rated the proportion of unique hues (top) or intermediate colors (bottom) for a complete set of colors; each panel shows predictions from Opponent-Colors Theory and the data, adapted from [63]. The data in the top panel are consistent with the Hering's Opponent-Colors Theory; the data in the bottom panel violates predictions of the theory because participants observed unique hues as composed of proportions of intermediate colors; for example, unique red was perceived as a combination of purple and orange (B) Distribution of color chips selected by English speakers (top) or monolingual Tsimane' speakers (bottom) tasked with picking the color chip that is neither reddish nor greenish, adapted from [131]. The experiment focused on yellow, the most consistent unique hue in classic studies, and it used a task thought to be effortless because the underlying processes are thought to be innate. Participants in both language groups first identified the best exemplars of their terms for red and blue/green. Answers are comparable across groups, showing that the Tsimane' understand the task instructions. But the selection of colors as neither reddish nor greenish were highly variable among the Tsimane', implying that the sense of unique yellow is not innate.

represented together. One might think that the lack of words for unique hues would speak against Opponent-Colors Theory, but the theory pertains to color encoding and appearance, not how colors are discussed. Color-encoding mechanisms are likely the same in all people with normal color-vision genetics, are functional without industrialization [66], and are similar for trichromatic nonhuman primates (who have no language) [67,68]. When asked to pick the color that is neither reddish nor greenish in an array spanning reds to greens, the Tsimane' do not pick focal yellow (or brown) as predicted by Hering's theory. Instead, they show tremendous variability (Figure 3B).

In related work, Somali speakers were asked to identify yellow samples that contain no red or green [11]. The Somali behaved similarly to English speakers, seemingly consistent with Hering's theory. But in another experiment, participants were asked to name the unique hues apparent in colors across the array. The results were very different for English versus Somali speakers, violating Hering's theory and supporting the idea that hue decomposition is lexical [69].

Perceptual properties of colors
Opponent-Colors Theory states that the unique hues are innate, which might suggest that they are consistent across observers, as Hering assumed. But there is tremendous variability in unique hue selections [33] (Figure 2B). Moreover, the settings for each unique hue are uncorrelated within observers, showing that the hues are not encoded jointly as stipulated by Hering's theory [70].

Many other perceptual results violate Hering's theory. The unique hues can be influenced by changes in environmental color statistics [71] and transient use of colored glasses [72]. Unique hues are not selected with lower variability than intermediate hues [73,74]; they do not appear more colorful and are insufficient to describe all colors [75,76]; they are not especially salient [77,78]; they are not necessarily exclusive [79]; they are not readily explained by cone ratios [80], or post-receptoral encoding [74], or looking behavior in infants [81]; and at least one unique hue (green) changes throughout life [82]. The unique hues vary depending on methodology [83], they are not predicted by afterimages [84], and they are not complementary (although Hering thought they were) [9]. The afterimage (and complement) of red is bluish-green (not green).

Another way to test Hering's theory is by asking how trichromatic nonhuman primates categorize colors. Three studies have attempted this. The first showed that macaques bin colors into 'red', 'green', 'blue', and 'yellow' as humans do [85]. But the categories were predefined, so the experiment suffers the same flaw as classic hue-cancellation studies. The second study tested for a category boundary between green and blue. One was found in humans but not monkeys [86]. The third study used a data-driven approach and found that macaques have two color categories, neither of which align with unique hues (they align with 'warm' and 'cool') [87].

Patterns of color naming
Hering sought to quell opposition to his theory by invoking language, asserting that 'language has simple names for [the unique hues] that are not borrowed from colored natural bodies' [2] (p. 109). It is now recognized that language is not a read-out of perceptual processes, and even unique-hue names likely derive from diagnostically colored stuff ('red' is related to words for blood). In addition, one cannot always map color terms across languages, probably because color concepts vary across cultures [88]. Failure to recognize this fact led William Gladstone to declare that the ancient Greeks were blue-blind because he found no Greek term mapping onto English 'blue'. In fact, the ancient Greeks had several words to describe blues in various contexts [89]. The idea of 'primitive' cultures, and that they are color deficient, is now recognized as racist [90]. Yet the notion that color-naming patterns provide evidence regarding innate mechanisms took root, popularized by Berlin

and Kay who proposed that all languages evolve on a predictable trajectory dictated by Hering's theory [91].

As with classic hue-cancelation studies, Berlin and Kay's experiment may have begged the conclusion it was trying to test, for the task required that participants use specified 'basic color terms' [92]. Two studies of nonindustrialized cultures obtained data without these task constraints. One study discovered that the Hazda people in Africa label orange chips more consistently than blue chips, which violates Hering's theory since orange is not unique [93]. The other study asked the Tsimane' of South America to name 80 color chips; some participants were required to use basic-color terms, while others were simply asked to 'describe the color chip to someone in your language' [94]. The data, analyzed in an information-theoretic framework, show that communication efficiency of color is surprisingly similar regardless of the instructions, so the analysis can be applied to the 110 languages in the World Color Survey [95]. Across languages, communication is less efficient for blue and green than for many colors including pink, orange, and beige, again violating Hering's theory. The color-naming studies imply either that color naming does not tell us much about how color is encoded by the brain, or that Opponent-Colors Theory is not how color is encoded, or both.

The psychological research shows that colors can be described without appeal to Opponent-Colors Theory, and there is nothing perceptually special about the unique hues. If we follow the data, Hering's theory must be rejected.

Utility-Based Coding
It is one thing to show a theory is invalid. It is another thing to reject it, because doing so requires a replacement [96]. We think that a replacement is emerging, which we call Utility-Based Coding. Germs of this idea can be found in the literature [10,59,94,97–100].

The first part of Utility-Based Coding interprets retinal physiology not as evidence of appearance mechanisms but as a solution to constraints imposed by a camera-type eye, a solution that provides an optimal representation of the retinal image [101]. Because the retina is a fixed distance from the lens, only some wavelengths can be in focus at a time (for any prism, short wavelengths bend more than long). This chromatic aberration poses a problem for a system under selective pressure to extract both chromatic and spatial information [102]. This pressure may explain the vast overlap in spectral sensitivity of L and M cones: light will be focused to the same degree for both classes of cone, affording good spatial resolution (S cones are sparse). The encoding of chromatic information therefore requires post-receptoral neurons that use cone opponency, together with normalization mechanisms, to amplify slight differences in cone responses. By this argument, cone opponency has little to do with appearance. Instead, it is a way of achieving both color and spatial vision from the same cone mosaic.

The second part of Utility-Based Coding invokes cone-opponent mechanisms as a substrate for subsequent stages of processing that compute behaviorally relevant information, including, ultimately, appearance. Thus Utility-Based Coding makes fundamentally different predictions from Hering's theory about the relationship between encoding mechanisms and appearance. Encoding mechanisms should not leave an obvious trace in perception, for color appearances are an output of the brain that tell us about the world not constraints of the input. Contrary to Hering's theory, the colors corresponding to the spectral tuning functions of the cones or the poles of the cone-opponent mechanisms are not expected to be salient – and they are not [103–105]. By this logic, the 'quirk of nomenclature' is not innocuous: the use of color names for descriptions of cones, cone-opponent mechanisms, and related color spaces steers us into

a dead end about the mechanisms of color appearance. The terminology begs the question of the mechanisms by specifying the output as input.

Utility-Based Coding is supported by neurophysiological data that implicates extensive cortical resources in color processing. Neural populations from V1 to V4 are optimized to extract spectral information using a multitude of narrowly tuned mechanisms [47,52,57]. The observation that red, green, blue, and yellow can be achieved from cone spectral tuning [106] is not inconsistent with Utility-Based Coding; indeed, all colors should be extractable from the cone functions. And beyond V4, there is as much high-level visual cortex engaged in color perception as in face recognition [55]. The function of these color-biased regions remains to be determined, but they likely provide a substrate for the sophisticated computations that use color in the service of behaviors such as categorization [107–109], foraging [110,111], and ultimately appearance.

Utility-Based Coding liberates neurophysiologists from a preoccupation of trying to find a substrate for Opponent-Colors Theory. Studies of neural mechanisms can focus on understanding how maximally useful representations of color are wired up [112], how the color-encoding mechanisms adapt to changing contexts and shifting behavioral demands [100], how they arise in development [81], and how other surface-appearance properties such as gloss, luster, and transparency are represented [113,114] (see Outstanding questions). As the field advances, neural network technology may be instructive regarding how color categories emerge without hardwiring. For example, networks trained on natural scenes –photographs taken by humans – form color categories that are not so different from those generated by people [115].

Behavioral data as evidence of Utility-Based Coding

According to Utility-Based Coding, color words (and preferences [116]) reflect the things we want to label, not how we see [93,94,97,99,117–119]. Anthropological work has long validated this idea. In Papua New Guinea, one Yélî Dnye term for 'black' derives from the name of a tree whose nuts are not black until they are roasted [117]. Indeed, all color terms probably reflect behavioral relevance, not limits of discrimination. The term 'orange' comes from the fruit, not the other way around. By Utility-Based Coding, it becomes unsurprising that universal patterns of color naming correspond to the color statistics of objects [58,94], because what we label is what we care about. The lack of consistently demarcated blue and green is then explained by a paucity of cool-colored objects [58]. Within a Utility-Based Coding framework, focal colors are optimal representatives of behaviorally important categories [120]. Color naming is the efficient tradeoff between the complexity and accuracy of the lexicon [99], because color naming is governed by the ideas the speakers need to communicate not how colors are encoded [121]. Variability in color-naming patterns across cultures is then explained by differences in the ideas that different cultures need to communicate [98,119], while similarities in color naming among languages likely represent universal behavioral significance, for example, daylight, foraging, and social signaling [122,123].

Utility-Based Coding distinguishes between Hering's Opponent-Colors theory, a linking proposition that is wrong, from Hering's opponent colors, a cognitive mapping strategy that is evidentially useful. But according to Utility-Based Coding, the navigating strategy is not predetermined by color-encoding mechanisms – the strategy is sufficient to describe colors but not necessary. Accordingly, Hering's Opponent Colors provide one of many possible ways of communicating color, just as English is not innate but one of many languages. Like a language, Opponent-Colors Theory derives its utility when widely used and experienced as reflexive, which can lead to a category error about its cause. Utility-Based Coding therefore seeks answers from behavior and cognitive theory (including lexical contributions), rather than neurophysiology, about why cultures

settle on the color-naming and color-mapping strategies they use [69]. One prediction is that opponent colors become useful when called to mind, either explicitly [124] or, we would argue, implicitly through task structure and western education [125]. Utility-Based Coding also makes imaginable mapping strategies besides Hering's opponent-colors [63].

Utility-Based Coding does not deny that some colors might take on elementary or special status. However, it stipulates that if some colors are special, their specialness should be attributed to meaningful structure in the world, structure that has utility [126]. For example, unique yellow and blue might be understood not in terms of constraints imposed by encoding mechanisms but in terms of sun and sky – environmental features of universal relevance [127]. Capturing meaningful structure must engage neural processes far beyond encoding because the relevant features might vary depending on context and behavioral goals. Utility-Based Coding, therefore, places cultural developments such as industrialization in a new light: industrialization might promote color utility [94], but industrialization might itself be driven by the potential utility of color [128]. From the perspective of Utility-Based Coding, the surprising diversity of color-adaptation mechanisms [8,100] are evidence of flexible sophistication, not limitations of the visual system.

Utility-Based Coding is a long way from formally connecting physiology and perception. But recent studies suggest a way forward. One study developed a compression theory of color naming [99]. This theory is the basis for a quantitative model integrating the shared psychophysics of color perception with language-specific communicative needs for colors [119]. The model is applied to an object-color statistics database [58,94], and experimental tests that could invalidate the model are described. Another study systematically examined contributions to color naming and suggests that capacity constraints and linguistic usage play a more substantial role than the visual environment [121]. These studies can be complemented by statistical analyses [129,130]. In these studies, Opponent-Colors Theory is, usefully, not a premise. Instead, the studies provide a quantitative data-driven framework for relating behavior, theory, and physiology.

Concluding remarks

Color has long been useful as a tool to understand mechanisms that bring about perception and cognition, and it continues to be so. In modern times, Hering's theory has been instrumental, for it focused attention on physiological processes as causes of color appearance. But after 150 years of testing, we can conclude that the theory is wrong. Introspection might have provided an entry point for understanding color appearance, but it can be misleading about causes. To take a familiar example: Aristotle thought the earth was the center of the universe because experience tells us the sun rises and sets. The experience of color is similarly a poor guide, for it can lead to a gross underestimate not only of the sophistication of color behavior but also of the neural resources required. It is time to let go of Opponent-Colors Theory as an idea for understanding how the brain turns light into Spanish Moss and Raspberry Blush. A new framework, Utility-Based Coding, has emerged as an alternative for understanding both perceptual and biological mechanisms of color, and it may prove useful in linking these two domains of knowledge.

Declaration of interests

No interests are declared.

Resources

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