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Issue: *The Year in Cognitive Neuroscience***Color consilience: color through the lens of art practice, history, philosophy, and neuroscience**

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Paintings can be interpreted as the product of the complex neural machinery that translates physical light signals into behavior, experience, and emotion. The brain mechanisms responsible for vision and perception have been sculpted during evolution and further modified by cultural exposure and development. By closely examining artists' paintings and practices, we can discover hints to how the brain works, and achieve insight into the discoveries and inventions of artists and their impact on culture. Here, I focus on an integral aspect of color, color contrast, which poses a challenge for artists: a mark situated on an otherwise blank canvas will appear a different color in the context of the finished painting. How do artists account for this change in color during the production of a painting? In the broader context of neural and philosophical considerations of color, I discuss the practices of three modern masters, Henri Matisse, Paul Cézanne, and Claude Monet, and suggest that the strategies they developed not only capitalized on the neural mechanisms of color, but also influenced the trajectory of western art history.

**Keywords:** cones; retina; V4; macaque monkey; Modernism; Matisse; Cézanne; Monet

*It is only after years of preparation that the young artist should touch color—not color used descriptively, that is, but as a means of personal expression.*<sup>1</sup>

*A great modern attainment is to have found the secret of expression by color.*<sup>2</sup>

HENRI MATISSE

**Introduction**

For Henri Matisse, painting was serious business. Naturally, he wore a suit to work. Matisse, an icon of modern art who “everyone agrees deserves the title of the century’s greatest colorist,”<sup>3</sup> lived in the south of France and often painted with a smock to protect his formal attire from sticky oil paint. Wearing a smock was an easy decision. But what about the decisions that followed? As Matisse so bluntly states, “Anyone who paints has to make choices minute by minute.”<sup>4</sup> Faced with a blank canvas, how did Matisse decide what marks to apply where and with what color? And how did these decisions go on to

shape the trajectory of art history? To some extent, the kind of marks one makes is inevitably determined by body mechanics: our arms are attached at a fixed point, the shoulder, and so any attempt at a straight line invariably results in a gentle curve.<sup>5</sup> The physical structure of our bodies therefore influences drawing practice—and these influences may extend to cognitive development, shaping how we think. Similarly, the way in which our nervous systems encode light signals necessarily determines what we see and how artists paint. An emerging field of research, vision and art, explores the interface between the neural mechanisms of vision and art.<sup>6–10</sup> An extension of this field, which I take up here, concerns the interaction between visual processing and art practice: how do the mechanisms of vision influence the decisions of the artist at work? And what do the strategies that artists employ in making their work tell us about brain function? While the work and comments of artists are not scientific documents, with appropriate sensitivity to their limitations, these materials may be useful in informing

our understanding of how the brain works. In this essay, I take up the relationship between painting and color vision.

People have been experimenting with paints and pigments for the entire history of human culture, and have therefore generated a lot of data. But the richest data has come relatively recently, following on the heels of the industrial revolution, which fueled the development of synthetic dyes and pigments and resulted not only in the wide availability of inexpensive pigments in the latter half of the 19th century but also in an expansion of the color gamut available to the artist<sup>11–14</sup> (see also Ref. 15). With the development of synthetic pigments, the use of particular colors was no longer restricted by the wealth of the artist or sponsor, who previously could flaunt their influence by commissioning pictures containing rare pigments like gold, or better, ultramarine blue made from rare lapis lazuli rock. By 1830, synthetic pigments were widely available. For example, manufactured ultramarine was being churned out by factories across Europe, following the invention in 1826 of an inexpensive method of production by Jean Baptiste Guimet in France and, independently, by Christian Gottlob Gmelin in Germany.<sup>11</sup> In the same way that a technical development, photography,<sup>a</sup> paved the way for one of the most creative periods of painting in art history, the development of synthetic pigments foreshadowed an explosion of possibilities for the use of color. In some sense, the only limitation on the use of color became our neural machinery.

From this perspective, paintings can be interpreted as the product of our brains, specifically as the product of all the complex neural circuits that translate physical light signals into behavior, experience, and emotion. The neural machinery of our brains has been sculpted by many influences, not only during a given individual's development, but also during the history of evolution. By closely

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<sup>a</sup>Some argued that photography would herald the end of painting, which shows how incompetent we can be at predicting the impact of technology on culture. "From today painting is dead," the French painter Paul Delaroche allegedly concluded in 1839 in response to the development of the daguerreotype photographic technique. Although there is no evidence that Delaroche actually said this, the sentiment has been repeated periodically ever since the middle of the 19th century.<sup>1</sup>

examining artists' practices and the paintings they make, scientists and art historians can collaborate to uncover clues to how the brain works and thereby gain insight into how the brain has been influenced by cultural history and, in turn, has shaped that history. Here, I describe some of the clever strategies that artists have used to paint in color, and examine how these strategies exploit and reveal the neural basis for color. In this essay, I will consider three titans of color, Paul Cézanne (1839–1906), Claude Monet (1840–1926), and Henri Matisse (1869–1954). The work of these artists certainly influenced the direction of art history. One theory, to which I return in the last section of this essay, is that the art-historical significance of these artists' work derives from the dynamic interaction between the artist and his work during its production, an interaction that is constrained by neural mechanisms of vision and visual feedback. To fully understand the influence of these artists on art history, one may therefore benefit from knowledge of the neural mechanisms of color, which may themselves be better understood in light of art's historical and philosophical considerations of color. One might then argue that art practice, art history, neuroscience, and philosophy have undergone a kind of consilience, and are dependent upon each other for a complete account of color.<sup>b</sup>

### Color in the world and in our heads

There are lively philosophical debates about color, concerning whether color is determined by some objective real-world criterion, or rather by the particularities of the viewer.<sup>18</sup> These debates have often boiled down to the uneasy question "do you see red like I see red?" Curiously, we rarely ask whether two people see an object as having the same shape. One standard account for the specialness of color rests on the argument that, unlike an object's shape, it cannot be determined objectively by a physical measuring device like a ruler; the measurements of a penny, for example, reveal it to be round, confirm-

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<sup>b</sup>The term "consilience" was popularized by Wilson,<sup>17</sup> and I use it to point to the productive intersection between arts and sciences. The various disciplines might not wholly agree, but it is not necessary that they do. Rather, my argument is that understanding will come through appreciation of the many facets of color revealed by many ways of knowing.

ing our perception of it as round. But this account is flawed on two counts: first, we actually can measure the physical basis for color almost as easily as we can for shape, by using a spectroradiometer to determine the relative fraction of different wavelengths reflected or emitted from a colored object or source. And second, although we may be able to measure the diameter of a penny, rarely is the two-dimensional retinal projection of the penny round; it is almost always an ellipse. Although the physical basis for both can be measured just as accurately, the relationship between these physical stimuli and the perceptions elicited by them would therefore seem to be as complicated in the case of shape as it is in the case of color. The question, then, is why our perception of the shape of the penny is considered universal (“it is round”), yet its color is up for debate (“do you see it as orange like I see it?”). I would argue that the discrepancy between our account of shape and color reveals something unique about color, but it is not that shape is physically measurable and color is not. The discrepancy suggests, instead, that color carries a qualitatively different behavioral valence than shape: we care more about the troubling relationship between the physical basis for color and our experience of it than we do about the relationship between the physics of object shape and our perception of shape. This special feature of color may rest on the fact that we come to know color only through our eyes and not through our muscles and fingertips, which are also used to ascertain shape. In any event, color’s specialness may account for the passionate debates that constitute the history of color vision research and continue to this day.

What is so special about color? Scientific studies have shown that humans (with normal trichromatic color) possess extraordinary color detection and discrimination abilities;<sup>19</sup> some claim that “color is what the eye sees best.”<sup>20</sup> So we can conclude that color is an important part of our visual experience.<sup>21</sup> But for what, exactly, is color important? Answers often focus on the relevance of color for object recognition (the “ripe fruit” argument<sup>19,22–24</sup>) and occasionally on the use of color for intraspecific communication (the “your face is red, you must be angry” argument<sup>25,26</sup>). The seemingly unquantifiable, qualitative aspect of color that these hypotheses miss is the fact that we *like* color.<sup>27</sup> Color, unlike other aspects of vision (with the possible exception of pleasant faces), appears to have a direct impact

on the limbic system. Although emotional reactions can be elicited from shapes (e.g., the outline of a snake), these associations are learned and do not have the same pop-out characteristic of color. Consider a field of 2s in which one “5” is distributed. To identify this unique character, people will typically use a time-consuming search strategy, interrogating each letter (“is this a 5?”). But if the “5” is red (and the distractor 2s are black), the 5 will pop out instantly. For this reason, color is considered a “low-level” or basic visual feature.

Color contributes directly to emotional state,<sup>28–31</sup> which may account for why sports teams with red uniforms win more often.<sup>32</sup> Moreover, people who lose color perception as a result of brain damage become profoundly depressed<sup>33</sup> (although it is obviously unlikely that impaired color is the root cause of most depression). Evidence in support of the intimate relationship between color and emotion/reward fell out of a study examining experimental deep-brain stimulation (DBS) for the treatment of intractable depression. Mayberg and her colleagues found that DBS in humans of a brain region implicated in depression, Area 25, resulted in elevations in mood and enhancement of color perception. Following DBS of Area 25, “all patients spontaneously reported acute effects including . . . sharpening of visual details and intensification of colors in response to electrical stimulation.”<sup>34</sup> The special status of color may underlie our use of color as a metaphor for emotion and a host of other ineffable experiences, such as musical timbre (often called “sound color”).

Although debates rage on in contemporary philosophy, there are some facts concerning color about which we have consensus. First, with the exception of imaginary colors, color is dependent on the spectral content (wavelength) of light reaching the eye from the outside world. But, as we will see, the relationship between our experience of an object’s color and this spectrum is not straightforward. While the color of monochromatic light viewed as a disc surrounded by black (“aperture color”) can be predicted,<sup>c</sup> it is difficult, if not impossible, to predict

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<sup>c</sup>White light, when split by a prism, is divided into a series of monochromatic wavelengths, each of which can be assigned a color term, from red, for the longest wavelengths, to violet, for the shortest wavelengths (ROYGBIV).

a subject's perception of a given stimulus given an objective physical measurement of the stimulus under natural viewing conditions. You might think that the color of an object could be determined by simply measuring the relative amount of each wavelength reflected from the object, but it cannot. Rather, the color we experience is contingent on the spatial and temporal context in which a stimulus is viewed, and these contextual relationships must be computed by the brain. This leads to a second conclusion of consensus: that our visual systems are implicated in encoding color. The responsible neural mechanisms not only transform light signals into electrical impulses that are the currency of the nervous system, but also generate spatial and temporal comparisons of the light signals across the visual scene and integrate these data with the viewer's expectations, shaped by development, experience, and cultural exposure. In coarse terms, these aspects of the neural machinery have been referred to as "bottom-up" and "top-down"; the former term describes the feed-forward, sequential processing of light signals along the visual pathway from the retina, through the thalamus, and up through various visual cortical regions, and the latter term refers to the influences of cognition and prior experience on the brain's calculation of what color is assigned to the feed-forward signals.<sup>35</sup>

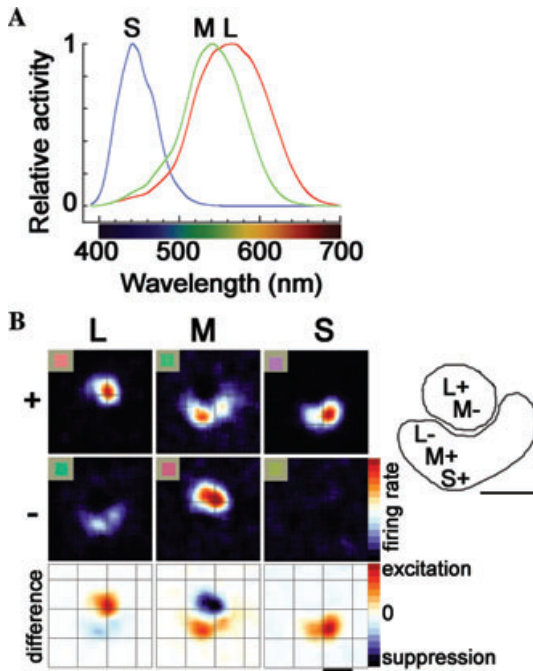
The neat division of processing mechanisms into bottom-up and top-down—a scheme that treats neural signals like batons passed from one runner to the next in a relay with a starting gun and a finish line—is a gross simplification that may turn out to be frankly wrong. Certainly, the spatial metaphor of a "line" of discrete "relays" is incorrect. Increasing evidence shows that brain regions are richly connected by feed-forward and feed-back connections that are engaged seemingly simultaneously,<sup>36–39</sup> so placing any brain region at a discrete "stage" in the processing hierarchy is questionable. A more apt analogy might be one of making soup: visual signals contribute to the perceptual output of the brain just as additional ingredients would shape the flavor of a soup, but their contribution to perception and behavior is influenced by the previous state of the brain and how strong the visual signals are in that context, just as the added flavor of any new ingredient is influenced by what else is in the soup. At the risk of pushing the analogy too far, spices would be the diffuse modulatory inputs, like those that regu-

late attention and wakefulness, which set the tenor for the whole operation. How bottom-up relays and top-down feedback, or cortical soup making are actually implemented in the brain in the service of color is anything but resolved. But once again there are areas of consensus, and new research using new techniques is shedding light on some stubborn questions, as discussed in the next section.

### Neural mechanisms for color

The retina contains three types of cone photoreceptor cells that are the first steps in the feed-forward computation of color (Fig. 1A). These cells do not encode primary colors, and the brain does not mix the activity of the cones as a painter might mix primary paints. Instead, to encode color, our brains have circuits that compute the relative amount of each type of cone activity across the visual scene. This spatial calculation enables the brain to achieve something called color constancy, the phenomenon that causes our experience of a given object's color to be stable despite changing illumination conditions.<sup>27,40–43</sup> Through color constancy, our brains enable us to see color as part of objects, not contingent on whether we are looking at them under a blue sky or a cloudy sky. These two different viewing conditions would change the physical spectral signals received by the eye, yet our experience of the color of an object does not change that much—fair weather or foul, we consider the apple to be red. For the mathematically inclined, the problem of color constancy can be summarized in straightforward terms:<sup>44</sup> the spectral signals that the eye receives from an object are the product of two variables, the spectral content of the illuminant<sup>d</sup> and the absorptive property of the object. As organisms that attained color vision for some selective advantage, the only thing we really care about is the property of the object—the ripe apple needs to be seen to be

<sup>d</sup>The spectral content of the illuminant describes the relative proportion of wavelengths across the visible spectrum that comprises an illuminant. A spectroradiometer can be used to measure the spectral content of the illuminant reflected off a standard "white" card. Natural daylight on a cloudless day has relatively uniform levels of light across the visible spectrum, and will contain a higher proportion of short-wavelength light than tungsten light, which has relatively low amounts of short-wavelength light and a large proportion of long-wavelength light.



**Figure 1.** The first stages in the neural encoding of color. (A) Cone-absorption spectra of the three classes of cones (L, M, and S) in the retina. (B) Receptive-field of a double-opponent cell in primary visual cortex. Top panels show the spatial receptive-field map generated using sparse noise cone-isolating stimuli and reverse correlation; difference maps show the “+” maps subtracted from the “-” maps. The insets give an indication of the color of each stimulus (although the actual stimuli were presented on a computer monitor and carefully color calibrated). Scale of the grid is 0.75° of visual angle. The receptive-field center was excited by an increase in L cone activity (L+) or a decrease in M activity (M-), and suppressed by a decrease in L (L-) or an increase in M (M+); the receptive-field surround gave the opposite pattern of chromatic tuning. The surround but not the center was modulated by S cones; the S response had the sign as the response to M cones. The diagram to the right provides a summary. Adapted from Refs. 50 and 51.

ripe under all viewing conditions for the experience of color to be evolutionarily advantageous. Because the spectrum of the various lighting conditions can vary enormously; the spectrum coming from the same object under different lighting conditions also varies tremendously. That the brain extracts a more-or-less constant color signal bound to objects despite this changing illumination is a remarkable achievement, one that even the most advanced cameras can only approximate.

The three cone types in the retina are called “L,” “M,” and “S,” because they have peak sensitivities in the long-, middle-, and short-wavelength regions

of the visible spectrum. Importantly, however, each cone type has a very broad absorption curve. In the case of the M and L cones, this means that light of virtually every wavelength from the shortest (or bluest) part of the spectrum all the way to the longest (or reddest) part of the spectrum can be effective at eliciting responses. The peak of both the M and L cone types, which historically have been loosely referred to as the “green” and “red” cones, is actually in the yellow part of the spectrum. It is sufficient to say that the rich spectral information hitting the retina is reduced to three numbers at any given retinal location: the amount of activity in the L, M, and S cones. These three signals are compared by retinal bipolar cells just one synapse downstream of the cones, in a process that is thought to involve two channels: one comparing L and M signals and one comparing S signals to the sum of L + M signals. These two channels are still referred to as “red-green” and “blue-yellow,” but these short-hand terms are inaccurate because the chromatic tuning of the neurons does not map onto the basic perceptual categories of red, green, blue, and yellow. The optimal chromatic stimulus for the “blue-yellow” channel, for example, is actually lavender-lime. To date, the neural basis for the basic perceptual categories is still unknown,<sup>45,46</sup> although there is some evidence that implicates specialized brain regions downstream of primary visual cortex in the visual processing hierarchy, as I will describe at the end of this section.

The cone-comparison signals encoded by the bipolar cells are converted into a digital signal of action potentials by the retinal ganglion cells, whose axons constitute the optic nerve that courses out the back of the eye and terminates in the lateral geniculate nucleus (LGN) of the thalamus, a structure composed of layers of neural tissue folding, or “gen-uflecting,” to form a peanut-sized structure located deep in the brain—you can almost touch it through the roof of the very back of your throat. Neurons of the LGN send their axons to primary visual cortex, the first cortical stage of visual processing, often called V-1 for short, and paradoxically located at the very back of your brain, as far away from the eyes as any part of the brain can be. Curiously, the LGN receives almost 10 times as many synapses from V-1 as it does from the retina.<sup>47</sup> Each one of these feed-back synapses is wimpy in comparison to the retinal feed-forward synapses, but one can already begin to see the limits of the “relay” analogy described

earlier: feedback begins before retinal signals even enter the cerebral cortex. The cortex has already started its soup.

Neurons in the LGN with color-coding properties were first described over 50 years ago in the macaque monkey, a creature who has virtually the same cone types and visual system as humans and has become the standard model of human color vision. Although LGN cells carry chromatic information, Hubel and Wiesel showed that the cells have a peculiar response property: they respond well to full-field colored light, but not to small spots of colored light on contrasting backgrounds. For example, a “red-on” cell would respond to full-field red but not to a red spot on a green background.<sup>48</sup> This is puzzling because it is at odds with what we know about color perception, namely that the color of full-field color, a *Ganzfeld*, is not very salient, while a spot of color on a contrasting background pops right off the page (or screen). Evidence for a spatial transformation of the color signals that could mediate color contrast is first found in V-1, manifest by a specialized population of neurons called double-opponent cells.<sup>49,50</sup> Double-opponent cells respond best to color boundaries, say a red region next to a green region. Each V-1 neuron receives inputs from a restricted patch of the retina which corresponds to a portion of the visual field. This small window on the world is called the cell’s “receptive-field.” An example of a double-opponent receptive-field is shown in Figure 1B. The cell derives its name from the fact that it consists of two kinds of opposition: chromatic and spatial. The chromatic opponency is manifest by opponent responses, excitation or suppression, to L and M cones, whereas the spatial opponency is manifest as opponent responses to the same cone type in spatially offset regions of the receptive-field. The cell shown in Figure 1B was excited most strongly by a reddish spot presented on a blue–green background. These cells encode local cone ratios, and their importance to color rests on the potential for them to mediate color constancy: note that the response of the cell is relatively unperturbed by a full field of light flooding both the receptive-field center and the receptive-field surround—any excitation caused by the stimulus in one receptive-field subregion is counteracted by suppression caused by the stimulus in the adjacent subregion. One can consider the spectral bias of an illuminant to be a full-field stimulus, affecting all parts of a scene; double-opponent cells,

which do not react to full-field stimuli, are therefore capable of discounting the spectral bias of the illuminant.

Double-opponent cells represent a small fraction of the total population of neurons in V-1, which initially led investigators to miss them and then to overlook their significance.<sup>51</sup> But importance is not always reflected in numbers: as Richard Gregory pointed out to me, a vivid chromatic signal was carried by a small fraction of the total bandwidth of the analog television signal (analog TV is now obsolete). The rest of the bandwidth of the analog signal was devoted to higher spatial resolution of black-and-white shapes.

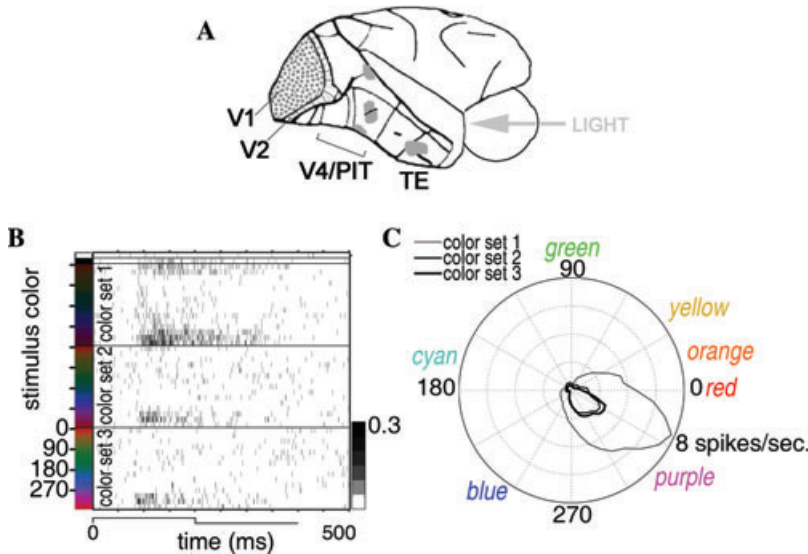
Neurons in V-1 besides double-opponent cells can also carry chromatic information (reviewed in Ref. 52), although it is less clear whether this information is used by the brain to encode hue *per se*, or rather used in the service of object recognition and motion perception. One can imagine that there would be a selective advantage for an ability to identify an object boundary formed by colored regions without encoding the colors forming the boundary—this ability is required to defeat camouflage in which the hue of the various regions comprising the object is actually distracting. Many neurons in V-1 show responses to colored boundaries regardless of the colors forming the boundaries, providing a potential neural substrate for this ability. But very few neurons in V-1 show sharp color tuning; that is, V-1 cells do not tend to respond exclusively to one color. Even a given double-opponent cell is not narrowly color-tuned for small spots presented in the center of the receptive-field. Instead the response properties of these cells are determined by the cone-contrast of the stimuli, which does not correlate directly with color perception: the cell shown in Figure 1B shows L versus M + S opponency. A stimulus that increases the activity of the L cones or decreases that of M cones appears red (bright or dark), whereas a stimulus that decreases the activity of S cones appears lime green and one that increases activity of the S cones appears lavender. The crescent-shaped receptive-field subregions of the cell shown in Figure 1B were excited by increases in the activity of M cones and decreases in that of L cones (both of which appear green), but also excited by increases in the activity of S cones (which appears lavender). The take-home message is that while these cells may contribute to color con-

trast calculations, clearly they are not by themselves encoding hue.

The functional properties and organization of the relatively large region of cortex devoted to vision outside of V-1 are still very dimly understood in comparison to our knowledge of V-1.<sup>53–57</sup> But broad consensus among experts is that V-1 is not the only cortical region involved in processing color: parts of the second visual area (V-2, immediately adjacent to V-1), large islands within the inferior temporal cortex (IT, a large swath of brain buried under the ears and on the bottom of the brain, which contains classically defined areas V-4, PIT, and posterior TEO), and regions of anterior TE (closer to the front of the brain) all contain neurons that respond preferentially to colored stimuli (Fig. 2A). But the first region beyond V-1 in which neurons with narrow hue tuning have been unequivocally described with single-unit recording (the “gold standard”) is PIT (Figs. 2B and 2C), and these neurons are densely clustered in millimeter-sized islands of tissue, dubbed “globs.”<sup>53</sup> Experimental estimates of the fraction of color-tuned neurons within the globs

approach 90%, which represents a remarkable level of specialization.

As a heuristic, one can consider each of the brain regions described here—retina, LGN, V-1, V-2, IT, and TE—to be involved in constructing a distinct aspect of the color percept.<sup>27,52</sup> The three cone types are the basis for trichromacy; retinal ganglion cells that respond in an opponent fashion to activation of different cone classes are the basis for color opponency; double-opponent neurons in V-1 generate local color contrast and are the building blocks for color constancy; glob cells in IT elaborate the perception of hue; and TE integrates color perception in the context of behavior. Certainly, this sketch is grossly simplified and likely inaccurate. We will need to make many more measurements to understand how the activity of neurons in the various stages relate to perception, and there will be much work unpacking how activity within the entire cortical color circuit influences the processing of incoming signals. But we are further ahead than we were 50 years ago when many scientists thought color could be read out directly from the response properties of LGN cells.



**Figure 2.** (A) Simple hierarchical, feed-forward model of color processing in the macaque cerebral cortex. Regions of cortex shown in gray, which increase in spatial scale along the visual-processing hierarchy from primary visual cortex (V1) to TE, are implicated in color processing. The first region beyond V-1 in which neurons with narrow hue tuning have been unequivocally described with single-unit recording is PIT, where these neurons are densely clustered in millimeter-sized islands of tissue, dubbed “globs.” Panels B and C show the color tuning of a typical glob cell. (B) Poststimulus time histograms to an optimally shaped bar of various colors. Responses were determined to white and black (top two rows in histogram) and various colored versions of the bar that varied in brightness. Stimulus onset aligned with 0 ms; stimulus duration (step at bottom). Gray scale bar is average number of spikes per stimulus repeat per bin (1 ms). (C) The color tuning to each of the stimulus sets in polar coordinates. Adapted from Refs. 52 and 53.

## Challenges in painting color

Color poses an enormous challenge for artists because the way a painted mark will ultimately appear is unpredictable. It may be this feature of color that led some artists, like Wassily Kandinsky, to ascribe mystical power to color. It led me to study the neural basis of visual perception in search of explanations. The difficulty of painting in color is juxtaposed with the relative ease with which novice students can acquire representational drawing skills, as Edwards' now classic text attests.<sup>58</sup> The challenge posed by painting in color is exacerbated by the fact that we often conceive of color in simple terms, as a superficial glazing overlaid on an achromatic world. This misconception is perpetuated by children's coloring-in books, which provide black outlines to relay the "important" information, and give deceptively simple instructions to select the appropriate color but to "stay within the lines"; some neuroscientists have characterized the neural encryption of color in these terms.<sup>59</sup>

Curricula at traditional art schools often mirror this process: students are first taught to draw with achromatic pencil lines and then, after mastering black-and-white, to work with paint (as Matisse advised in the epigram quoted at the beginning of this essay). Although this approach may make the problem of representation seemingly tractable, it fosters a misunderstanding of the mechanics of color. The apple in the still life may appear red, but the redness, and our reaction to it, are not attributed solely to the pigment in the skin of the apple, nor can that redness be captured entirely (or even adequately) by matching that pigment with paint. Rather the color is attributed to an unconscious comparison that the visual system makes between the color of the apple, the color of the surrounding regions, and the context in which we see the apple—the very same comparisons that form the basis for color constancy.<sup>e</sup>

<sup>e</sup>The challenge was articulated by Matisse: "If upon a white canvas I set down some sensations of blue, of green, of red, each new stroke diminishes the importance of the preceding ones. Suppose I have to paint an interior: I have before me a cupboard; it gives me a sensation of vivid red, and I put down a red that satisfies me. A relation is established between this red and the white of the canvas. Let me put a green near the red, and make the floor yellow; and again there will be relationships between the green or

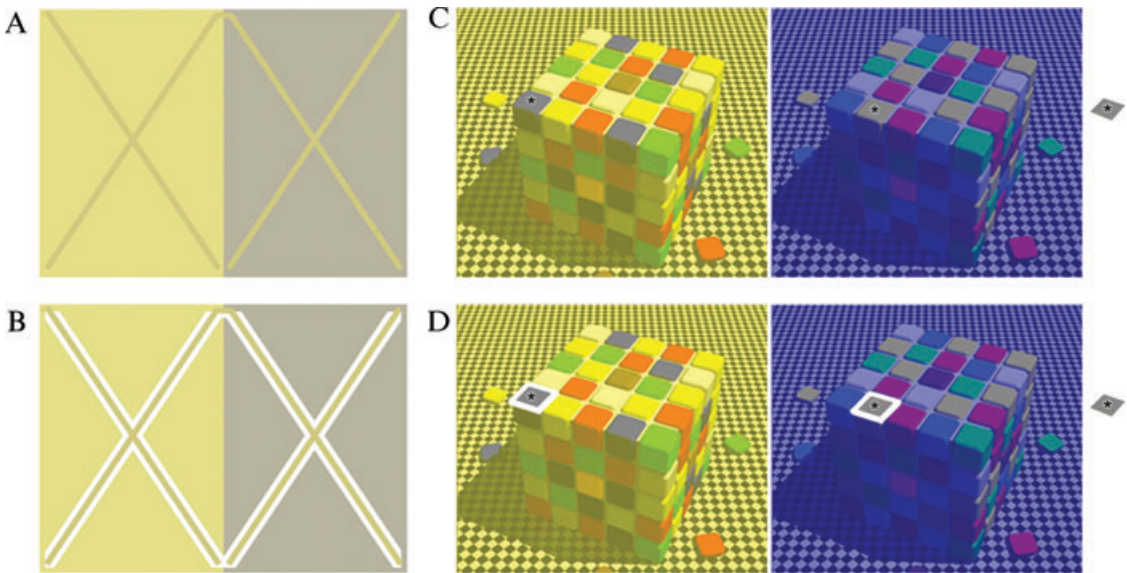
For whatever reason, our visual system hides this computation from our awareness and leaves us only with an impression that the color is immutable and attached to the object that is the focus of our attention. The consequence is that when confronted with a blank sheet of paper and asked to paint—in color—the apple, we instinctively reach for the tube of red paint, and pay little attention to the background and other viewing conditions. Art teachers find themselves perennially repeating the mantra: "Don't forget about the background!" To which the student retorts: "I'll get to it when I'm done painting the apple." But the application of a background does not have a neutral effect on the work-in-progress, and the surprised and disappointed student is suddenly grossly displeased with the color of the apple, a color that was perfectly satisfactory when floating on the raw white canvas. The experience reinforces the student's resistance to painting backgrounds, and keeps alive the art teacher's mantra.

What accounts for the sudden decline of the painting, coincident with work on the background? The explanation must have something to do with the fact that the student has an impression in his or her mind's eye, a color memory of the object presumably stored deep in brain area TE, which does not match the painting in front of him or her. The dissatisfaction that the student experiences during this exercise underscores how important context is to our experience of color,<sup>f</sup> and how little we acknowledge context in anticipating our experience of color. In the case of color, the spectral bias of the illuminant plays a large role in establishing the

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yellow and the white of the canvas which satisfy me. But these different tones mutually weaken one another. It is necessary that the diverse marks [signes] I use be balanced so that they do not destroy each other." (see Ref. 2, p. 40).<sup>f</sup> Color is determined by the context in which it appears, its relationship to the whole, and by the quantity of it within the picture (although this relationship does not bear in a straightforward way on the color). These considerations contribute to the "quantity-quality" calculations described by Bois (1993), and as Bois argues quite compellingly, "The founding principles of Matisse's art proceed from the fact that color relations, which determine expression, are above all relations between surface quantities" (see Ref. 3, p. 23). Thus, Bois argues, Matisse's drawing is determined by the same principles as his color, in service of the same goal of personal expression.





**Figure 3.** Color interaction depends on immediately adjacent colors. The “X” target in panel A has the same spectral reflectance in both panels, yet appears a different color because it is placed on a colored background (adapted from Ref. 75). This effect is demonstrated again in panel C (courtesy of Beau Lotto). Panels B and D show that the color induction effect is obliterated by insulating the target with an achromatic margin.

context for color judgments, and as described earlier, we are virtually blind to the spectral content of the illuminant; this blindness is in very effective service of color constancy. The artist’s frustration is therefore a direct consequence of the fact that we evolved to see color, not to paint it. Matisse and other artists indicate cultural progress in this regard, as Matisse clearly acknowledged, “Each color in the painting was determined by and dependent on the others,”<sup>60</sup> and as Bois goes on to reinforce, “Matisse was constantly forced to start from scratch because each color stroke implied a further dissonance, ricochet-like, and necessitated an unsettling of the picture’s global color harmony.”<sup>61</sup>

The neglect of context is not unique to perceptions of color: the anticipated emotional reaction we have to a given event is radically impacted by the context in which the event is experienced, although we rarely pay much attention to these effects.<sup>62</sup> Color, like a mental preview of a future event, is essentialized, defined by salient aspects and largely agnostic of context. We define color by its category (red, orange, yellow, green, and blue), one that may have behavioral or linguistic relevance. But the context, as the art student’s experience shows, is ignored despite the fact that context significantly shapes not

only our color experience, but also our emotional reaction. This complexity makes the task of artists particularly difficult, for they must uncover the unconscious mechanisms that underlie color in order to be able to paint in color.<sup>63</sup>

The context dependence of color means that the colored elements comprising the scene interact; and the neural basis for these interactions almost certainly depends to some extent on the calculations made by double-opponent cells. The interaction of color constituted the primary focus of the artist and teacher Josef Albers (1888–1976), whose powerful images underscored the disjunction between what we think underlies a color and the role of context. Figure 3A shows one of Albers’ famous color induction demonstrations. In this image, Albers is employing a simple color contrast effect to alter the appearance of a line by placing the line against different colored backgrounds. The image remains surprising even though we fully understand the power of color context to shape our color experience. And all the information in the world is still insufficient to stave off the question, “But what color is the line in reality?”—as if our eyes have deceived us on this rare occasion. Rather than deception, these demonstrations showcase what the visual system is constantly

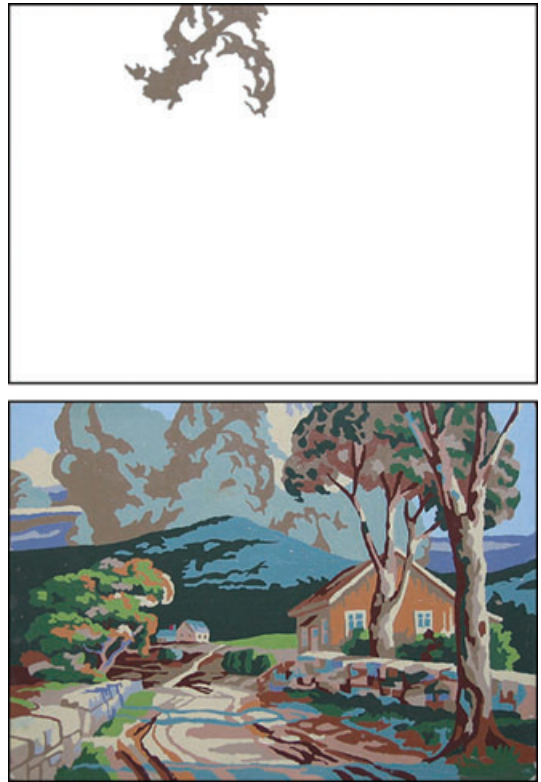
doing—and usually to great adaptive effect—by taking context into account, and then discounting that very information. Such contrast effects continue to inspire the development of powerful demonstrations, like Beau Lotto’s cube shown in the Figure 3C. These contextual interactions continue to be mined for clues to the operation of the visual system.<sup>64–66</sup>

Why is it so difficult to learn how to render perceptually accurate color? There are probably several reasons, but I think the main one has to do with the fact that the color computation is effortless. The automatic nature of color leads us to believe that there is a straightforward relationship between the physical stimulus (photons off the apple, and paint in the artist’s case) and the color experience. This is reflected in the instructions often given to art students. Indeed, when I took art courses at university, this was the instruction I received: identify a patch of color in the scene, mix it on your palette, and apply it at the appropriate location on the canvas. The instruction sounds logical but it is deeply flawed. One mixes the color on a gray or white palette and applies the paint to a canvas that is white or gray (at least to start) yet the color is ultimately viewed in a colored context. If one were asked to paint Lotto’s cube, one might logically begin by painting the yellow squares with paint that appears yellow on the raw white canvas, instead of using paint that appears gray. This false start would influence all subsequent color decisions, and the outcome would consist of profoundly distorted color relationships.

Painting color accurately requires access to information that is simply not available to our perceptual apparatus, which may be why paint-by-number kits are so compelling (Fig. 4). Putting a milky greenish-brown patch in the sky does not seem like the right thing to do at the outset of the project, yet somehow the color is appropriate in the context of the completed image. Working through the painting becomes a kind of joke, in which the punch line (what color the marks appear to have in the finished picture) is surprising.

### Color-master strategies

So how do the painters we think of as masterful colorists capture perceptually accurate color relationships, and what do their strategies tell us about how the nervous system functions? The very category of “colorist” was generated within modern art tending toward abstraction. As painters turned from the



**Figure 4.** Paint-by-number image, partially completed (top panel), and finished (bottom panel).

strictures of representation that photography had mastered, they were liberated to focus on color, a more recondite aspect of perception. Perhaps we can get some insight into this conjoined project involving both culture and the nervous system from the artists’ unfinished works. The left panel of Figure 5 shows a painting that Paul Cézanne was working on at the time of his death. What is striking about it is the lack of a defined subject. Unlike the academic painters of his day, Cézanne does not begin with a well-resolved preparatory line drawing; instead, he begins the work almost immediately with intensely colored paint, and continues to develop the image with patches of color distributed over the surface of the painting. We can begin to make out the suggestion of tree trunks, foliage, sky, and earth—many of the cues to such suggestions are purely coloristic. Using this approach, Cézanne recruits his visual system as a meter of accurate color. Importantly, he has given up the natural conviction that the color of the patch is stable throughout the



**Figure 5.** The visual system as feedback device used to paint color: Paul Cézanne (1839–1906; French) Study of trees 1904 Oil on Canvas; Mont Ste.-Victoire seen from les Lauves [V.798; R.912] 1902–1906.

development of the image. He is able to alter the color through adjacency, by adapting and modifying the painted context in which a colored patch appears. Specifically, he alters the colors of his marks by adding surrounding colors, changing their appearance through changes in context. The approach allows a form of evolution: Cézanne creates a diversity of marks, and then progressively emphasizes those that are the most effective—that most accurately capture his perceptual color experience—and de-emphasizes those that are least effective, by changing their context or occasionally covering a patch with a different color. As the marks on the canvas suggest, this is a dynamic and unpredictable process in which the decision of what colored patch to apply next is largely prescribed by local circumstances—what mark he makes is determined by what is needed to compensate for the change in color appearance of all the marks on the canvas caused by the mark just made. Although the trajectory of the painting may be set (a painting of trees), Cézanne does not seem to be attempting to reproduce a completed picture he has in his mind's eye at the outset of the painting. Rather, the precise combination of colors and marks he uses is made up on the spot and guided continually by visual feedback.

Many colorists have worked in a similarly empirical fashion, developing paintings through trial and error. Perhaps the most famous is Claude Monet, an exemplar well known to Cézanne, who made painting *au plein air* enormously popular in the 19th century. This approach to painting supposedly involves making pictures of scenery outside under natural light, directly looking at the subject being painted.

On first blush, this appears to be a similar approach to that used by Cézanne for it would seem to encourage direct visual feedback. So I was surprised to learn that most of Monet's early finished paintings were completed in his studio. (This is, incidentally, a delightful historical example of how the rhetoric produced around art often precedes the art actually made that way.) The painting shown in Figure 6, for example, was begun *au plein air*, but completed some months later in his studio, in winter. Without a real-life scene immediately before him, Monet completed the image through many local decisions, errors, and corrections reflected in the thick layers of paint of the finished picture. Beginning the image *au plein air* honed Monet's observational skills and presumably refined his color memory, and it was this memory that provided stable feedback during the development of the painting in studio. Paradoxically, this feedback might have been more stable than if the scene lay before him in life because real-world scenes are constantly changing, the light shifting throughout the day with a time course shorter than the time required to paint. In his later career, Monet would shift from canvas to canvas throughout the day actually painting *au plein air* before the same motif, making numerous sets of paintings of haystacks and cathedrals that document the passage of time and the changing play of light throughout the day. As a result of his careful observation, and the time spent in studio critically assessing the success of his attempts, Monet was able to reproduce color boundaries as they move through shadow in a way that reflects the cone ratios generated by real color boundaries moving in and out of shadow. It



**Figure 6.** The visual system as feedback device used to paint color: Claude Monet (1840–1926). *Femmes au jardin* (Women in the Garden), started spring/summer 1866 open air in Ville-d’Avray, finished the following winter in studio Honfleur. Collection Musée D’Orsay, Paris (RF2773) Oil on canvas.

is these local cone ratios that are encoded by the visual system and form the neural building blocks for color. It remains a testable hypothesis whether the cone ratios elicited by the color boundaries in Monet’s paintings are similar to those encoded by the nervous system, perhaps by double-opponent cells.

I do not want to suggest that all masters of color work in the same way. Indeed, Monet’s early practice is manifestly different than the later methods of Cézanne, although they lived at more or less the same time and painted some of the same motifs in France. In fact, it is the inventiveness of the artist’s

solution to the problem of color that contributes to the visual interest of their work, and their lessons for neuroscience. Consider the artist with which we began, also recognized for his stunning use of color: Henri Matisse. A striking feature in many of Matisse’s mature canvases, beginning in early 1904, is that he leaves portions of the raw canvas untouched. These white regions typically fall at the interface between two differently colored marks. Figure 7 shows **three** examples dating from 1905 to **1948**; the spare use of paint, in contrast to the slathered thick overlapping marks deployed by Monet, was a consistent feature of Matisse’s process, one also

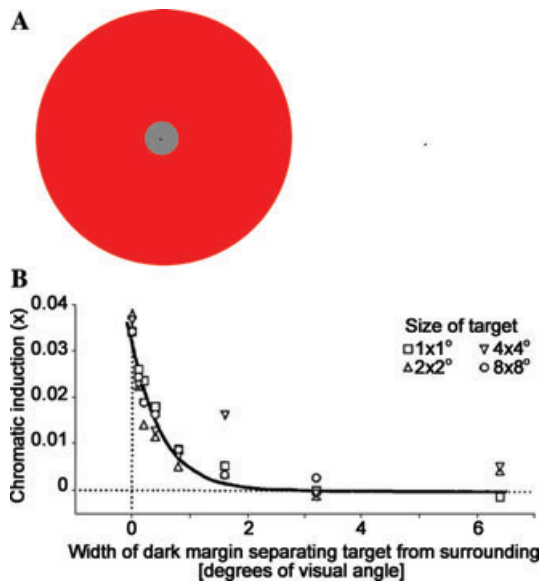


**Figure 7.** The use of achromatic borders to separate colored regions in paintings of Henri Matisse. Henri Matisse (1869–1954; French): *Intérieur à Collioure/La sieste* (Interior at Collioure/The Siesta), Oil on canvas, 23 1/4" × 28 3/8" Private collection, 1905 (left panel). *Poissons rouges et sculpture* (Goldfish and Sculpture) spring–summer 1912, oil on canvas 45 3/4" x 39 1/2" Museum of Modern Art, NY (right panel).

exploited by Cézanne.<sup>8</sup> Moreover, most of Matisse’s canvases were signed, confirming for the art market that Matisse considered them finished works; the white omissions were clearly intended.

What lay behind Matisse’s intention? A clue is provided by some classic psychophysical work reviewed by Brenner and his colleagues:<sup>67</sup> “It is known that chromatic induction is primarily determined by the color of directly adjacent surfaces. . . This is consistent with the idea that information at the borders is critical in determining the perceived color.” Chromatic induction is the Yin of the chromatic contrast Yang: it is the phenomenon whereby a target that appears an achromatic gray when placed

<sup>8</sup>The importance of the white unfinished spaces to the color relationships was quite obvious to Cézanne, as demonstrated with his exchange with the art dealer and critic Vollard, as Bois recounts, “What Cézanne said to Vollard concerning the two small spots on the hands in his portrait that weren’t yet covered with pigment: ‘Maybe tomorrow I will be able to find the exact tone to cover up those spots. Don’t you see, Monsieur Vollard, that if I put something there by guesswork, I might have to paint the whole canvas over starting from that point?’” Bois goes on to emphasize that “Matisse was well aware that the apparently ‘unfinished’ quality of Cézanne’s canvasses had an essential function in their construction.”<sup>61</sup>



**Figure 8.** Color induction is eliminated when achromatic boundaries separate an otherwise achromatic target from the colored surround. The panel shows induction in the x direction (red–green) of the cone space of MacLeod and Boynton as a function of the distance between the border of a target and the colored surround; similar effects are seen in the y direction (blue–yellow). Adapted from Ref. 68.



**Figure 9.** The development of color in the later paintings of Henri Matisse accentuates their inherent flatness. Henri Matisse (1869–1954; French).

on a white (or black) background will appear colored when surrounded by a color field; the induced color is the complementary color of the background. Figure 8A gives an example in which the “gray” central disc appears greenish; curiously, the induced color is often stronger as an afterimage: maintain your gaze on the black dot in the center of the disc, then after 10 seconds transfer your gaze to the black dot to the right. Most observers report the appearance of a striking red spot that is the afterimage to the induced green. Figure 8B, adapted from an original paper by Ref. 68, shows that the degree of color induction (indicated along the  $y$ -axis) falls off precipitously if the target is separated from the surrounding colored field by an achromatic margin. I have illustrated this observation using the powerful Albers and Lotto demonstrations shown in Figures 3B and D. Given the importance of these local interactions, it is perhaps not surprising that Albers always painted his color fields immediately adjacent to each other. The prediction from Albers is that color is dependent on neural calculations that take place over small local spatial scales, comparable to the spatial scale of double-opponent receptive-fields, which compare the relative cone ratio in one part of visual space with the cone ratio in an immediately adjacent region of visual space.

Let’s return to Matisse. Whether he was conscious of it or not, the small achromatic, white gaps left by Matisse would have insulated the appearance of the

colors against color induction during the development of the image. As a result, the marks Matisse made remain largely the color he chose them to be at the time he made them. In this way, Matisse was liberated to use vibrant saturated colors, often right out of the tube, without the fear that his colors would become garish from chromatic contrast. The desire to use saturated colors is pervasive, suggesting deep roots in our neural hardware. And the consequence of Matisse’s strategy for protecting against induction was, I wager in the next section, an important driving force in the trajectory of art history and the development of Modernism.

### **Painting practice, new materials, and Modernism**

Beginning with his fauvist work in the early 1900s and extending for the rest of his career, Matisse’s output represents a pinnacle of Modernism and owes its success in large part to his innovative use of color.<sup>2,69,70</sup> One consequence of Matisse’s dedication to color, in the reading of historians and theorists of modern art, is the accentuation of the inherent flatness of a painted surface. Compare two paintings that bookend Matisse’s long career (Fig. 9). In the early painting, Matisse seems to struggle to achieve a representation of perspective and depth; the colors he uses are subsidiary. In the later painting, the color is fundamental and more playful, but the image lacks depth, appearing instead as a decorative wall panel not unlike



**Figure 10.** The use of achromatic borders to separate colored regions in paintings of Max Beckmann. Max Beckmann (1884–1950; German): Self portrait in blue jacket 1950, 54 3/4" x 36" The Saint Louis Art Museum (right panel). Bequest of Morton D. May. Oil on Canvas Self Portrait in Florence, 1907 (left panel).

a carpet with broad areas of uniform color enlivened by small graphical marks. Without addressing the cultural considerations as to why Matisse might have sought this flatness, the consensus is that he achieved it. The development of color in this later work, as already described for the images shown in Figure 7, involves a sparing use of paint that leaves bare portions of the underlying canvas, particularly at boundaries between colored regions. As described earlier, this strategy insulates Matisse's color choices against color induction during the process of painting, so the colors we see in the final painting are presumably very close to the colors Matisse decided upon when the picture was being created. Matisse's simple strategy of limiting color induction by leaving white margins around the colored marks was adopted by many other Modernists, including Wassily Kandinsky, Milton Avery, Mark Rothko, and later Frank Stella, whose "pin-stripe" paintings launched his career in 1959 with their pulsating whispery white "breathing lines," the remnant unpainted white buffers between broadly painted black stripes (Ref. 71 discussed in Ref. 72). Others, like Max Beckmann, employed a variant: the use of heavy black lines (Fig. 10), which serve the same purpose. Like Matisse, Beckmann began his career attempting to capture space and depth,

but concluded by painting images whose color and flatness are central. In these cases, the vivid flatness of the work would seem to be attributed to an emphasis on color because color is for the most part a surface property: the surface of the painting is flat, a fact we come to be aware of through its color.<sup>h</sup> Indeed, the neural mechanisms of color are tied up with the neural mechanisms responsible for encoding surfaces and textures.<sup>73</sup> This attribute of color may, incidentally, account for the philosophical claim that color is tied to objects.

Modernism characterizes a broad movement in thought and culture in Western society that culminated sometime between the end of the 19th century and the middle of the 20th century. It is during this time that the role of subjective experience in art making and interpretation becomes significant. The grand subjects that were often the basis for pictures made during the Renaissance until the French Revolution, such as history, kings, queens, discoveries,

<sup>h</sup>Some have argued for a different spatial register to account for the visual experience of colors deployed in intangible screens, like the sky, a smoky sunset, or a cave wall indirectly illuminated by a fire; whether these colors are experienced as surfaces is perhaps debatable.

and conquests, are rarely the focus of Modernist pictures. (Modernists tended to break with the academy that persisted with those themes.) Instead, we find depictions of domestic life, intimate scenes that underscore the interaction of the artist and his subject. The work showcases the involvement of people with their new-found self-consciousness. These trends have been exhaustively described in the extensive literature on Modernism. Here, I shift focus to question the relationships between the artist, her materials, and her artistic process—which I construe broadly to include the dynamic interaction between the artist and her work during its development, an interaction that is inextricably characterized by the neural mechanisms of vision and visual feedback. These relationships evolved during Modernism and have continued to be a central force in art making today.

The flatness of Matisse's work advanced the Modernist agenda by drawing attention to the material properties of the work: Matisse's work proclaims itself to be objects made of paint and canvas, rather than mere depictions of scenes. As Wright suggests, Matisse "is becoming more interested in paint than in sight."<sup>70</sup> Matisse's focus on color, and on the material properties of paintings, set the stage for high Modernist masters like Mark Rothko and Barnett Newman, whose mature canvases are entirely abstract, consisting simply of large swaths of bold uniform color. Matisse's work is a bridge between one side "the eye of Impressionism or Neo-Impressionism, all eager regard, scanning the shifting surfaces of the world, and on the other, the eye of modernist visuality, absorbed in the formal qualities of a the painting's own surface."<sup>70</sup> I argue here, Matisse's accomplishment was brought about in part because of the particularities of his practice, one aspect of which sought to insulate color from induction. The result of this particular strategy, those vacant bits of canvas, revealed what the paintings were made of; and as a consequence, the making of paintings, rather than their content, took center stage. As Elderfield describes it, the "substance of painting itself came to fulfill the functions that form and structure had fulfilled earlier";<sup>69</sup> see also Ref. 74.

Matisse's paintings are not appreciated as illusions of real space, but rather as objects whose power to move us, much like the power of color itself, is difficult to pin down. The power of Matisse's pic-

tures surely rests on a successful use of color; and this use of color derives its success in part from the process Matisse adopted in making the pictures, a process that was contingent on the particularities of his practices, and their probing relation to the neural mechanisms of color. In the case of the example described here, the decision to leave portions of the canvas unpainted may be attributed to a practical desire to mitigate color induction; but the consequence of this decision pulled back the curtain on the process of art making itself and emphasized the materials of art, thereby underscoring the subjective experience of the artist as art maker, actively engaged in the making of an object.

Matisse's interest in color propelled his rejection of tradition, a tradition that aimed not only to represent objects in space and depth but also to subjugate the materials of painting—brush, paint, and canvas—to the requirements of mimetic representation. Matisse's approach freed painting from this traditional requirement, and is justly celebrated for that liberation. The artist makes the painting self-conscious by underscoring its own making. The viewer cannot escape appreciating that the painting is made of paint and canvas: we have direct evidence of these facts, revealed in many of his paintings by vacant white lines across their surfaces. Thus, it seems that Matisse's sensitivity to color and the innovative process he developed to make his pictures, helped to advance one important aspect of the Modernist agenda: the desire to achieve an accurate representation of the artist's subjective experience of color.

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## Conflicts of interest

The author declares no conflicts of interest.

## References

1. Wolff, T.F. Drawings of Matisse. *N.Y. Christian Science Monitor*, 25 March 1985, p. 27.



2. Flam, J. 1995. *Matisse on Art (Revised Edition)*. University of California Press. Berkeley and Los Angeles, CA: p. 121.
3. Bois, Y.-A. 1993. Matisse and "Arche Drawing." In *Painting as Model*. MIT Press. Cambridge, MA: p. 61.
4. Flam, J. 1995. *Matisse on Art (Revised Edition)*. University of California Press. Berkeley and Los Angeles, CA: p. 101.
5. Van Sommers, P. 1984. *Drawing and Cognition: Descriptive and Experimental Studies of Graphic Production Processes*. Cambridge University Press. New York.
6. Cavanagh, P. 2005. The artist as neuroscientist. *Nature* **434**: 301–307.
7. Conway, B.R. & M.S. Livingstone. 2007. Perspectives on science and art. *Curr. Opin. Neurobiol.* **17**: 476–482.
8. Livingstone, M.S. 2002. *Vision and Art: The Biology of Seeing*. Abrams Press. New York.
9. Zeki, S. 1999. *Inner Vision: An Exploration of Art and the Brain*. Oxford University Press. New York.
10. Marmor, M.F. & J.G. Ravin. 2009. *The Artist's Eyes: Vision and the History of Art*. Abrams Books. New York.
11. Roy, A., Ed. 1993. *Artist's Pigments: A Handbook of Their History and Characteristics, Volume 2*. National Gallery of Art. Washington, DC.
12. Feller, R.L., Ed. 1986. *Artist's Pigments: A Handbook of Their History and Characteristics, Volume 1*. National Gallery of Art. Washington, DC.
13. Fitzhugh, E.W., Ed. 1997. *Artists Pigments: A Handbook of Their History and Characteristics, Volume 3*. National Gallery of Art. Washington, DC.
14. Berrie, B.H., Ed. 2007. *Artists' Pigments: A Handbook of Their History and Characteristics, Volume 4*. National Gallery of Art Washington, DC.
15. Douma, M. 2011. Pigments through the ages. URL <http://www.webexhibits.org/pigments> [accessed on 15 August 2011].
16. Crimp, D. 1981. The end of painting. *October* **16**: 69–86.
17. Wilson, E.O. 1998. *Consilience: The Unity of Knowledge*. Knopf. New York.
18. Byrne, A. & D.R. Hilbert. 1997. Colors and Reflectances. In *Readings on Color Volume 1: The Philosophy of Color*. MIT Press. Cambridge, MA: pp. 263–288.
19. Gegenfurtner, K.R. & J. Rieger. 2000. Sensory and cognitive contributions of color to the recognition of natural scenes. *Curr. Biol.* **10**: 805–808.
20. Chaparro, A., et al. 1993. Colour is what the eye sees best. *Nature* **361**: 348–350.
21. Hurlbert, A. 1997. Colour vision. *Curr. Biol.* **7**: R400–402.
22. Dominy, N.J. & P.W. Lucas. 2001. Ecological importance of trichromatic vision to primates. *Nature* **410**: 363–366.
23. Smith, A.C., et al. 2003. The effect of colour vision status on the detection and selection of fruits by tamarins (*Saguinus* spp.). *J. Exp. Biol.* **206**: 3159–3165.
24. Caine, N.G. & N.I. Mundy. 2000. Demonstration of a foraging advantage for trichromatic marmosets (*Callithrix geoffroyi*) dependent on food colour. *Proc. R. Soc. Lond. B* **267**: 439–444.
25. Changizi, M.A., Q. Zhang & S. Shimojo. 2006. Bare skin, blood and the evolution of primate colour vision. *Biol. Lett.* **2**: 217–221.
26. Fernandez, A.A. & M.R. Morris. 2007. Sexual selection and trichromatic color vision in primates: statistical support for the preexisting-bias hypothesis. *Am. Nat.* **170**: 10–20.
27. Conway, B.R. 2009. Color vision, cones, and color-coding in the cortex. *Neuroscientist* **15**: 274–290.
28. Valdez, P. & A. Mehrabian. 1994. Effects of color on emotions. *J. Exp. Psychol. Gen.* **123**: 394–409.
29. Adams, F. & C. Osgood. 1973. Cross-cultural study of affective meanings of color. *J. Cross. Cult. Psychol.* **4**: 135–156.
30. Ou, L. et al. 2004. A study of colour emotion and colour preference. Part I: Colour emotions for single colours. *Color Res. Appl.* **29**: 232–240.
31. Gao, X., et al. 2007. Analysis of cross-cultural color emotion. *Color Res. Appl.* **32**: 223–229.
32. Attrill, M.J., et al. 2008. Red shirt colour is associated with long-term team success in English football. *J. Sports Sci.* **26**: 577–582.
33. Sacks, O. & R. Wasserman. 1987. The case of the colorblind painter. *N.Y. Rev. Books* **34**: 25–34.
34. Mayberg, H.S., et al. 2005. Deep brain stimulation for treatment-resistant depression. *Neuron* **45**: 651–660.
35. Gregory, R.L. 1998. *Eye and Brain: The Psychology of Seeing*. Oxford University Press. Oxford.
36. Lamme, V.A., H. Super & H. Spekreijse. 1998. Feedforward, horizontal, and feedback processing in the visual cortex. *Curr. Opin. Neurobiol.* **8**: 529–535.
37. Hupe, J.M., et al. 1998. Cortical feedback improves discrimination between figure and background by V1, V2 and V3 neurons. *Nature* **394**: 784–787.
38. Angelucci, A., et al. 2002. Circuits for local and global signal integration in primary visual cortex. *J. Neurosci.* **22**: 8633–8646.
39. Bullier, J., et al. 2001. The role of feedback connections in shaping the responses of visual cortical neurons. *Prog. Brain Res.* **134**: 193–204.
40. Land, E.H. 1977. The retinex theory of color vision. *Sci. Am.* **237**: 108–128.
41. Brainard, D.H. & B.A. Wandell. 1986. Analysis of the retinex theory of color vision. *J. Opt. Soc. Am. A* **3**: 1651–1661.
42. Kraft, J.M. & D.H. Brainard. 1999. Mechanisms of color constancy under nearly natural viewing. *Proc. Natl. Acad. Sci. USA* **96**: 307–312.
43. Hansen, T., S. Walter & K.R. Gegenfurtner. 2007. Effects of spatial and temporal context on color categories and color constancy. *J. Vis.* **7**: 1–15.
44. Stockman, A. & D.H. Brainard. 2010. Color vision mechanisms. In *OSA Handbook of Optics*. 3rd ed. M. Bass, Ed. McGraw-Hill. New York.
45. Valberg, A. 2001. Unique hues: an old problem for a new generation. *Vision Res.* **41**: 1645–1657.
46. Webster, M.A., et al. 2000. Variations in normal color vision. II: Unique hues. *J. Opt. Soc. Am. A. Opt. Image Sci. Vis.* **17**: 1545–1555.
47. Briggs, F. & W.M. Usrey. 2010. Corticogeniculate feedback and visual processing in the primate. *J. Physiol.* **589**: 33–40.
48. Wiesel, T.N. & D.H. Hubel. 1966. Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey. *J. Neurophysiol.* **29**: 1115–1156.

49. Michael, C.R. 1978. Color vision mechanisms in monkey striate cortex: dual-opponent cells with concentric receptive fields. *J. Neurophysiol.* **41**: 572–588.
50. Conway, B.R. 2001. Spatial structure of cone inputs to color cells in alert macaque primary visual cortex (V-1). *J. Neurosci.* **21**: 2768–2783.
51. Conway, B.R. & M.S. Livingstone. 2006. Spatial and temporal properties of cone signals in alert macaque primary visual cortex. *J. Neurosci.* **26**: 10826–10846.
52. Conway, B.R., et al. 2010. Advances in color science: from retina to behavior. *J. Neurosci.* **30**: 14955–14963.
53. Conway, B.R., S. Moeller & D.Y. Tsao. 2007. Specialized color modules in macaque extrastriate cortex. *Neuron* **56**: 560–573.
54. Conway, B.R. & D.Y. Tsao. 2006. Color architecture in alert macaque cortex revealed by FMRI. *Cereb. Cortex* **16**: 1604–1613.
55. Harada, T., et al. 2009. Distribution of colour-selective activity in the monkey inferior temporal cortex revealed by functional magnetic resonance imaging. *Eur. J. Neurosci.* **30**: 1960–1970.
56. Yasuda, M., T. Banno & H. Komatsu. 2010. Color selectivity of neurons in the posterior inferior temporal cortex of the macaque monkey. *Cereb. Cortex* **20**: 1630–1646.
57. Tanigawa, H., H.D. Lu & A.W. Roe. 2010. Functional organization for color and orientation in macaque V4. *Nat. Neurosci.* **13**: 1542–1548.
58. Edwards, B. 1979. *Drawing on the Right Side of the Brain*. Penguin Putnam. New York.
59. Gegenfurtner, K.R. & D.C. Kiper. 2003. Color vision. *Annu. Rev. Neurosci.* **26**: 181–206.
60. Flam, J. 1995. *Matisse on Art (Revised Edition)*. University of California Press. Berkeley and Los Angeles, CA: p. 62.
61. Bois, Y.-A. 1993. Matisse and “Arche Drawing.” In *Painting as Model*. MIT Press. Cambridge, MA: p. 48.
62. Gilbert, D.T. & T.D. Wilson. 2009. Why the brain talks to itself: sources of error in emotional prediction. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **364**: 1335–1341.
63. Hurlbert, A. 2007. Colour constancy. *Curr. Biol.* **17**: R906–907.
64. Lotto, R.B. & D. Purves. 2000. An empirical explanation of color contrast. *Proc. Natl. Acad. Sci. USA* **97**: 12834–12839.
65. Shevell, S.K. & F.A. Kingdom. 2008. Color in complex scenes. *Annu. Rev. Psychol.* **59**: 143–166.
66. Purves, D., W.T. Wojtach & R.B. Lotto. 2011. Understanding vision in wholly empirical terms. *Proc. Natl. Acad. Sci. USA* **108**(Suppl 3): 15588–15595.
67. Brenner, E., et al. 2003. Chromatic induction and the layout of colours within a complex scene. *Vision Res.* **43**: 1413–1421.
68. Brenner, E. & F.W. Cornelissen. 1991. Spatial interactions in color vision depend on distances between boundaries. *Naturwissenschaften* **78**: 70–73.
69. Elderfield, J. 1979. Describing Matisse. In *Henri Matisse: A Retrospective*. J. Elderfield, Ed.: 14. Museum of Modern Art. New York.
70. Wright, A. 2004. *Matisse and the Subject of Modernism*. Princeton University Press. Princeton and Oxford.
71. Genauer, E. 16-artist show is on today at Museum of Modern Art. *New York Herald Tribune*, 20 December 1959.
72. Jones, C.A. 1998. *Machine in the Studio: Constructing the Postwar American Artist*. University of Chicago Press. Chicago: pp. 407–408.
73. Lu, H.D. & A.W. Roe. 2008. Functional organization of color domains in V1 and V2 of macaque monkey revealed by optical imaging. *Cereb. Cortex* **18**: 516–533.
74. Gowing, L. 1979. *Matisse*. Oxford University Press. New York: p. 59.
75. Albers, J. 1975. *Interaction of Color Unabridged Text & Selected Plates*. Yale University Press. New Haven.