

Relative Absorption Model of Color Vision

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Received 23 October 2003; revised 13 August 2004; accepted 20 October 2004

Abstract: Opponent processing is widely accepted as providing a general framework for the standard model of human color vision. After the cones' responses are transmitted to second stage neurons, however, there is no consensus on exactly how synaptic connections are organized. The Relative Absorption Model introduced here is an explicit neural network that generates neural correlates of color vision. The model makes detailed predictions of known color and neural phenomena, including familiar aspects of color perception. Until now these phenomena have not had an explicit neural explanation. The model's simplicity shows that color does not require complex processing of spectral information. The network receives excitatory and inhibitory input from three classes of spatially proximate photoreceptors with different spectral sensitivities. Four second stage neurons provide symmetric input to four third stage neurons, whose outputs are correlates of red, green, blue, and yellow. These color cells identify which receptor type has the greatest absorption of photons and which has the least. Their response intensities correspond to the differences between those absorptions and the middle absorption. A single second stage neuron computes violet and purple information that is then transmitted through the red and blue channels, the only channels in the network capable of conveying the information. Five additional neurons produce correlates of black and white. The white cell's response intensity measures the smallest of the three absorptions, and the black response measures how far the largest absorption is from full saturation. © 2005 Wiley Periodicals, Inc. *Col Res Appl*, 30, 252–264, 2005; Published online in Wiley InterScience (www.interscience.wiley.com). DOI 10.1002/col.20121

Key words: color vision; neural model; neural correlates; neural network; opponent colors; opponent processing

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INTRODUCTION

Attempts to explain the mechanisms of color vision extend back to ancient Hindu, Greek, and Arab philosophers, and interest in understanding color undoubtedly existed much earlier. Although it had been known since antiquity that most colors can be produced by mixing a small number of pigments, the trichromacy theory of color is usually attributed to Thomas Young. He said that three classes of retinal “particles” capable of “vibrating” with three principal colors are sufficient to produce all the perceived colors.¹ Ewald Hering pointed out that the trichromacy theory does not explain the mutually exclusive color pairs, red–green and blue–yellow.² Hering believed his opponent theory accounted for these qualities of color by supposing each pair is transmitted through one neural channel in opposing kinds of signals.

The famous and often heated debate over the two theories persisted for nearly a century. Several models attempted to integrate the two theories with trichromacy at the sensory level and opponent processing at the second stage.³ That approach seemed to be supported by the discoveries of three different pigments in the cones^{4–6} and opponent-color neurons that are activated by photostimuli of one color and are suppressed by the opponent color.^{7,8} Since then many models have been proposed to explain color and related neural phenomena.^{9–19} Although trichromacy is firmly established at the sensory level and opponent processing is widely accepted as providing a general framework for the standard model of color vision, there is still no agreement on an explicit neural model that produces neural correlates of color perception.²⁰

An explicit neural network that generates neural correlates of color vision may explain how receptors and neurons are connected to process sensory information and generate perceptions. This is a significant difference from other types of models that have been proposed. Three-dimensional color figures and mathematical models such as Maxwell's color triangle²¹ and the CIE system describe perceived colors. Several partial neural models with a few synaptic

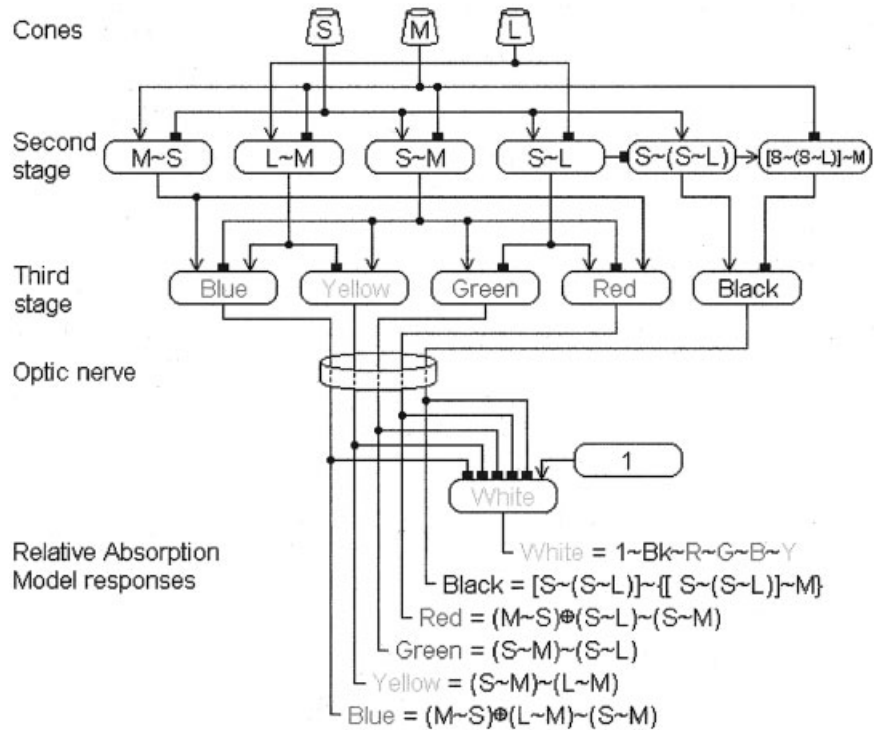


FIG. 1. Relative Absorption Model circuit diagram. The network receives input from three classes of spatially proximate photoreceptors with different spectral sensitivities. The six outputs are neural correlates of color vision. Arrows indicate excitatory input, blocks indicate inhibitory input. If X and Y are the intensities of two output signals, X~Y represents the output intensity of a neuron with excitatory input X and inhibitory input Y. If both inputs X and Y are excitatory, the output is denoted by X ⊕ Y.

connections rely on unspecified networks later in the visual pathway to work out the details of color perception. No matter how accurately these models describe perceptions, they cannot explain how neurons create them.

The neural network presented here may resolve the question of how synaptic connections are organized to process spectral information. To distinguish this model from others, it will be referred to as the Relative Absorption Model (RAM). The RAM is explicit, simple, and symmetric. Known color and neural phenomena follow directly from the network's architecture and the minimal cellular properties of excitation and inhibition. The RAM's properties do not depend on assumptions of sophisticated or unknown cellular capabilities. The RAM does not require information to be encoded in opposite kinds of signals, an assumption central to the opponent theory. The RAM shows that mutually exclusive colors and opponent-color neurons, as well as other phenomena, can be explained with fewer assumptions. The RAM also makes predictions of more phenomena and in greater detail than has any explicit version of the standard model.

The RAM is meant to be an initial component of the visual system and as such is not meant to explain all color phenomena. Spatial phenomena necessarily depend on input from spatially separated cones, which the RAM does not have, and on additional neural structure to process this information. The RAM's structure is consistent with the three main layers of retinal cells, and evidence suggests spatial phenomena are not produced in the retina.²² Temporal phenomena are not discussed here because standard explanations of most temporal phenomena also apply to the RAM. Temporal phenomena are determined mainly by cellular properties and other mechanisms of the eye. The main

differences between the RAM and the various versions of the standard model lie in the synaptic connections' organizations, which have little effect on most temporal phenomena.

This article defines the RAM and derives its main properties. A few color and neural phenomena are discussed briefly to illustrate how the RAM generates them. The RAM's outputs identify the cones with the largest and smallest absorptions of photons and, as the model's name implies, measure these absorptions relative to the middle absorption and relative to the maximum and minimum possible absorptions. These outputs transform sensory data into neural correlates of color and black and white, and they provide correlates of hue, saturation, and brightness. Violet and purple information is transmitted through the red and blue channels, the only RAM channels that can accomplish this without a considerable loss of information. The RAM's color cells make chromatic color distinctions, and the RAM explains the achromatic characteristics of black and white. The RAM responses make up a geometrical color space that provides detailed, quantitative neural explanations of standard color figures such as Newton's color wheel and Munsell's color system. Explanations are also given for the continuous yet categorical nature of color, mutually exclusive colors and colors that can be perceived together, color mixing, the Bezold-Brücke hue shift, the additivity failure of brightness, and opponent-color cells.

THE NEURAL NETWORK

Figure 1 shows the RAM's cells and their synaptic connections. The network receives input from three classes of spatially proximate photoreceptors with different spectral

sensitivities. Six neurons produce the network's outputs, which are labeled red, green, blue, yellow, black, and white. These cells' responses are neural correlates of color vision. This means a photostimulus causes the RAM's red cell to respond if and only if that stimulus causes a person with normal vision to see red. The correlations also account for combinations of colors and their relative strengths. A photostimulus elicits a strong response from the RAM's yellow cell and a weak response from the green cell if and only if that stimulus is seen as yellow with some green content. Correlates of hue, saturation, and brightness are defined later in terms of the RAM responses. The correlations do not preclude the possibility that under some conditions such things as spatial contrast can modulate or transform the RAM output signals by further processing later in the visual pathway. Perceptions and sensations do not need to be defined here. What must be demonstrated is that a photostimulus ordinarily described as a greenish-yellow hue also causes the RAM's green and yellow cells to respond in the right proportion, a photostimulus normally described as a highly saturated color also has a high RAM saturation value, and so on.

Output signals from receptors and various types of neurons have different physical natures and are generated by different physiological processes. The significant characteristics from a signal processing perspective are that the intensity of the stimulus is reflected in the receptor's response, and this intensity is carried over in the signal's transmission from receptor to neuron and from neuron to neuron. Output signals consisting of all-or-nothing action potentials encode this intensity in the frequency of action potentials. The response intensity is assumed to be measured at some moderate level of adaptation. Since temporal phenomena are not considered here, that adaptation level does not vary. Such mechanisms as pupil constriction and shifting the focus of attention after brief time periods may keep most cells at a moderate level of adaptation most of the time. The only requirement here is that the RAM cells are not so fully adapted that their responses are independent of input.

For convenience, signal intensities are normalized by dividing them by the maximum possible intensity for the given level of adaptation. This puts signal intensities in the interval from 0 to 1, with 0 meaning no signal and 1 meaning the maximum intensity. This number will be called the *response* of the receptor or neuron. If a neuron's response is not zero, the neuron is said to *respond*. The responses of three proximate photoreceptors sensitive to short, medium, and long wavelengths are represented by *S*, *M*, and *L*. Italicized letters *S*, *M*, and *L* represent the numbers of photons absorbed. Where convenient, these absorptions will also be normalized to values in the interval [0, 1], with 0 meaning no absorption and 1 meaning more photons do not affect the cone's response. A receptor's or neuron's output signal can be transmitted to more than one neuron, and each synapse can be either excitatory or inhibitory. If the responses of two photoreceptors or neurons are *X* and *Y*, the notation $X \sim Y$ will represent the response of a neuron

with excitatory input *X* and inhibitory input *Y*. If both inputs are excitatory, the response is denoted by $X \oplus Y$.

The white cell in Fig. 1 shows input from a neuron with response 1. An output signal that is constantly 1 could be provided by a special purpose neuron that fires spontaneously and continuously. Such neurons are known to exist.²³ They keep people awake, and sleep apparently requires inhibition of these neurons.²⁴ One such neuron could provide excitatory input to the white cells of several RAM networks. Alternatively, the white cell itself could be such a neuron with only inhibitory input from the other RAM cells.

Figure 1 illustrates the model in its simplest form. Retinal neurons actually have convergent input, especially in the periphery. The partial exception occurs in the fovea, where there is apparently only one cone at the center of the receptive fields of both bipolar and ganglion cells. Except for this case, each cone in Fig. 1 represents input from several neighboring cones of the same class. Each second stage cell in the figure can also represent several cells that have similar input but from different cones. In addition, cones and second stage neurons can provide input to different RAM networks with overlapping receptive fields. For example, a single S~M neuron could provide input to the color cells in several networks that have input from different L cones. The obvious candidates for the RAM's second and third stage neurons are the bipolar and ganglion cells. For receptors and second stage cells to excite and inhibit neurons at a distance, their signals may require transmission by intermediate cells. This function is likely carried out by horizontal cells in transmitting the cones' signals and possibly by amacrine cells at the next stage. For the sake of simplicity, these intermediate signal carriers are not shown in Fig. 1.

MAIN PROPERTIES

To show the RAM generates color phenomena, some minimal assumptions on cellular behavior are needed. Table I lists these cellular characteristics, which are merely a somewhat rigorous way of saying the intensity of the output is related to the intensities of the excitatory and inhibitory inputs in the obvious ways. The simplicity of the individual cellular properties shows the RAM's properties do not depend on assumptions of sophisticated or unknown cellular capabilities. The properties that say responses are increasing or decreasing functions are understood to hold on the intervals where the responses are between the minimum and maximum possible responses. Here "increasing" and "decreasing" refer to the fact that input and output intensities are variables. They are not increasing and decreasing with time. The RAM is entirely defined by Fig. 1. Although Table I is used to derive the RAM's properties, it is not part of the RAM.

For the conclusions of this article to hold for a RAM network constructed of real cells, the properties listed in Table I only need to be approximations of actual complex neural responses. Little information is available for the behavior of the neural response function $X \sim Y$, for example.

TABLE I. Cellular response properties.

<ol style="list-style-type: none"> 1. $1 \sim 0 = 1$. 2. $X \sim Y = 0$ if $X \leq Y$. 3. $X \sim Y$ is increasing in X. 4. $X \sim Y$ is decreasing in Y. 5. $1 \oplus X = X \oplus 1 = 1$. 6. $0 \oplus 0 = 0$. 7. $X \oplus Y$ is increasing in X and Y. 8. $0 \oplus X \sim Y = X \sim Y$ and $X \oplus Y \sim 0 = X \oplus Y$. 9. Cone response is 1 if absorption is 0, and the response is 0 if absorption is 1. 10. Cone response is a decreasing function of the number of photons absorbed. 11. Cell responses are continuous functions of input. 	<p>Maximum excitation elicits maximum response. Inhibition cancels equal or smaller excitation. Greater excitatory input increases output. Greater inhibitory input decreases output. The maximum response is 1. No input elicits no response. Greater excitatory input increases output.</p>
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The properties of the Relative Absorption Model follow from these cellular characteristics. Cone absorptions and cellular response intensities are normalized to be in the interval from 0 to 1.

Even for $X \sim 0$, the response to excitatory input only, the closest experimental approximations have depended on electrical current to simulate excitatory input. Property 2, for instance, may actually be $X \sim Y = 0$ if $g(X) \leq Y$ for some function $g(X)$ that only loosely approximates the identity function $I(X) = X$. Such small changes in the properties given in Table I would modify the conclusions about the RAM only by degrees; they would not negate the conclusions. To avoid confusion, a point should be made about cone response. Depolarization causes the release of transmitters that excite or inhibit neurons. Although depolarization is the response of most sensory receptors to the appropriate stimulus and the response of neurons to excitatory stimulation, depolarization in photoreceptors of vertebrates is inversely related to photon absorption. This is reflected in properties 9 and 10 of Table I.

The RAM's main properties are given in Tables II and III. These properties follow from the cellular characteristics of Table I and the RAM's architecture of Fig. 1. The first column in Tables II and III lists the possible orderings of three photon absorptions. The pairs of color names in Table II are simply descriptive names to distinguish the six ways three absorptions can be ordered by strict inequalities. The first word conveys which absorption is largest, the second word says which is smallest. Red means L is the largest absorption, yellow means S is smallest, etc. The six names are meant to provide an intuitive and mnemonic way of referring to the orderings, but for now the names themselves make no claims about perception. For each absorption ordering in the first column of Tables II and III, the second column lists the RAM's color cells that respond. To illustrate the argument, suppose the absorption ordering for some long wavelength photostimulus is $S < M < L$. The response ordering is $L < M < S$ by property 10 of Table I. By property 4, $S \sim L > S \sim M$ and $(S \sim L) \sim (S \sim M) > (S \sim L) \sim (S \sim L)$. The last expression is 0 by property 2. That is, $(S \sim L) \sim (S \sim M) > 0$. By property 2, $M \sim S = 0$, and by property 8 the red cell response is $(M \sim S) \oplus (S \sim L) \sim (S \sim M) = (S \sim L) \sim (S \sim M) > 0$. The last two columns of Table III show the RAM responses to binary

absorptions. These responses are easily computed from properties 1, 2, 8, and 9 of Table I.

The RAM produces a rather remarkable transformation of the sensory data. Simply by responding, the green cell identifies M as the largest absorption. This identification is unambiguous in the sense that it is independent of the magnitude of the response. The response magnitude measures the difference between M and the second largest absorption in the sense that the response is 0 if the difference is 0, the response is 1 if the difference is 1, and the response increases if the difference increases in either of its endpoints. This measure is independent of which absorption is second largest. Similarly, the yellow cell responds when S is the smallest absorption, and its response magnitude measures the difference between S and the second largest absorption independently of which absorption is second largest. Except when both the red and blue cells respond, a red cell response identifies L as the largest absorption and measures the difference between L and the second largest absorption, and a blue cell response identifies L as the smallest absorption and measures the difference between L and the second largest absorption. When both the red and blue cells respond, they still identify the relative position of L . In this case $M < S$, and L is the largest, middle, or smallest absorption if red $>$ blue, red = blue, or red $<$ blue, respectively. The white cell measures the smallest absorption, and black measures how far the largest absorption is from full saturation. These values are independent of which absorption is smallest or largest.

It is useful to see the RAM responses assuming the receptor and neural response functions are linear approximations of the actual responses. For these approximations, the excitatory input of $M \sim S$ to the red and blue cells is assumed to be at half strength as explained in the next section. The resulting RAM responses are easily computed and are listed in the third column of Tables II and III as approximate responses. The graphs in the fourth column of Table II illustrate example absorptions and the approximate RAM responses. The approximate white response $\min\{S, M, L\}$ stands for the smallest of S, M , and L , and

TABLE II. Relative Absorption Model responses to absorption orderings with strict inequalities.

Absorption order	Color cells that respond	Approximate RAM responses White = $\min \{S, M, L\}$, Black = $1 - \max \{S, M, L\}$	
Red-Yellow $S < M < L$	Red, Yellow	$R = L - M$ $Y = M - S$	
Green-Yellow $S < L < M$	Green, Yellow	$G = M - L$ $Y = L - S$	
Green-Blue $L < S < M$	Green, Blue	$G = M - S$ $B = S - L$	
Violet-Blue $L < M < S$	Red < Blue	$R = (S - M)/2$ $B = (S - M)/2 + (M - L)$	
Violet-Purple $M < L < S$	Red = Blue	$R = (S - M)/2$ $B = (S - M)/2$	
Red-Purple $M < S < L$	Red > Blue	$R = (S - M)/2 + (L - S)$ $B = (S - M)/2$	

The absorption orderings are listed in the first column, and the second column shows which color cells respond to each ordering. The third column gives the approximate response magnitudes using linear approximations to neural responses. The graphs in the last column illustrate example absorptions and approximate RAM responses.

$\max \{S, M, L\}$ is the largest of $S, M,$ and L . Tables II and III show the sum of the approximate RAM responses is 1 for every photostimulus. Only these approximations depend on the additional assumptions of linear neural responses and reduced strength of the $M \sim S$ signal. The other RAM properties in Tables II and III follow from the cellular properties given in Table I.

The RAM may explain why spectral information is processed in the retina. The properties listed in Tables II and III show the color cells identify the cones' absorption ordering. By property 10 of Table I, the cones' responses accurately reflect the absorption ordering but in the opposite order. If the cones' responses were transmitted to the brain, additive noise and signal attenuation in the long channels could change the ordering, especially if two absorptions are equal or nearly equal. If identifying the absorption ordering is an important function of vision, spectral information may be processed in the retina to avoid such errors.

For the RAM responses to be neural correlates of color

vision, it remains to be demonstrated that for each absorption ordering in the first column of Tables II and III, the perceived color can be described according to the second column. The degree of perception should also correspond to the approximations of the third column. For example, the RAM predicts that if a photostimulus has moderate S and L absorptions, with S slightly greater than L , and M close to full saturation, then the photostimulus will appear to be a slightly bluish green with some whiteness.

Violet and Purple Information

The RAM processes violet and purple information differently from other spectral information. The violet content of a triple of absorptions (S, M, L) is defined here as the difference between S and the second largest absorption if S is the largest absorption, and it is defined to be zero otherwise. The purple content is defined as the difference be-

TABLE III. Relative Absorption Model responses to special absorption orderings.

Absorption order	Color cells that respond	Approximate response	Binary (S, M, L)	RAM response
$S = M < L$	Red	$L - M$	(0, 0, 1)	Red = 1
$S = L < M$	Green	$M - L$	(0, 1, 0)	Green = 1
$L < S = M$	Blue	$S - L$	(1, 1, 0)	Blue = 1
$S < M = L$	Yellow	$L - S$	(0, 1, 1)	Yellow = 1
$M = L < S$	Red = Blue	$(S - M)/2$	(1, 0, 0)	Red = Blue
$M < L = S$	Red = Blue	$(S - M)/2$	(1, 0, 1)	Red = Blue
$S = M = L$	No color cell responds.	Black = 1 - L White = L	(0, 0, 0)	Black = 1
			(1, 1, 1)	White = 1

This table shows the RAM responses when two or all three of the absorptions are equal. For the first four orderings, the color response is the correlate of the appearance of unique red, green, blue, or yellow.

tween M and the second largest absorption if M is the smallest absorption and zero otherwise. There are several possible ways to compute and transmit this information, and the RAM's method is possibly the simplest.

The RAM could have included separate violet and purple color cells to measure and transmit the violet and purple information. Either $(M \sim S) \sim (M \sim L)$ or $(L \sim S) \sim (L \sim M)$ could serve as a violet response in the sense that either responds when S is the largest absorption and its response magnitude measures the difference between S and the second largest absorption. Similarly, either $(M \sim S) \sim (L \sim S)$ or $(M \sim L) \sim (S \sim L)$ could serve as a purple response, responding when M is smallest and measuring the difference between M and the second largest absorption. Psychophysical evidence, however, shows violet and purple information is transmitted through the red and blue channels rather than through two separate color channels, possibly because there was never selective pressure to obtain the full violet and purple information contained in the separate channels. Some information is necessarily lost in transmitting the information through other color cell's channels.

The most obvious way of transmitting the violet and purple cells' outputs through the red and blue channels might appear to be to transmit each through a separate channel. For example, the violet cell's output could be excitatory input to the blue cell and the purple cell's output could be excitatory input to the red cell. This cannot carry the information successfully because there would be no way to distinguish violet information from blue or purple infor-

mation from red. Both outputs must be transmitted to both cells. This does quite well in preserving violet and purple information, especially if the inputs are weighted. Since the violet and purple cells' outputs must be transmitted through both the red and blue channels, just one signal that carries the total violet and purple information as input to the red and blue cells might do as well or nearly as well. Checking each absorption ordering, it is easily seen that the total violet and purple content is $S - M$ if $S - M > 0$, and the total content is zero otherwise. The response $M \sim S$ measures this total violet and purple content in the sense that $M \sim S = 0$ if $S - M \leq 0$, $M \sim S = 1$ if $S - M = 1$, and $M \sim S$ increases if $S - M$ increases in either of the variables S or M . Figure 1 shows the RAM transmits the $M \sim S$ signal through the red and blue cells.

The RAM's red and blue channels are suitable for carrying the violet and purple information, and using any other RAM channels would result in a considerable loss of information. Transmitting the violet and purple information through a pair of color cell channels that are otherwise mutually exclusive avoids ambiguity in the meaning of the signals. Without the $M \sim S$ input shown in Fig. 1, the RAM's red and blue cells would be mutually exclusive because red would respond when L is largest and blue would respond when L is smallest. There are two design considerations favoring the RAM's red and blue channels over the RAM's other two mutually exclusive pairs, red-green and blue-yellow. First, Table II shows that transmitting the violet and purple information through the red and blue cells makes

discrimination of the three violet and purple absorption orderings possible by the relative magnitudes of the red and blue responses. The RAM's other two mutually exclusive pairs of color cells do not permit this discrimination of absorption orderings. If the violet and purple information is transmitted through the RAM's red and green channels, for example, it would be the only input to both channels for both the violet–purple and violet–blue orderings. This would make the two orderings indistinguishable. Second, only the red and blue cells have no inhibitory input when the absorptions have violet or purple content. For the red–purple ordering $M < S < L$, for example, the RAM's green cell response $(S \sim M) \sim (S \sim L)$ has inhibitory input $S \sim L$ and no excitatory input. If the purple information is transmitted through the green cell, the inhibitory input would reduce or even eliminate the effect of the excitatory purple input.

Transmitting the violet and purple signal $M \sim S$ through two channels might distort the information contained in the signal. Since both the red and blue channels inhibit the white cell, violet information transmitted through them would reduce the white response more than a signal carried in a single violet channel. To avoid this situation, the $M \sim S$ excitatory synapses at the red and blue cell neurons may have reduced strength. This is not an unreasonable supposition physiologically. Neurons have evolved with synapses that excite in a wide variety of ways.²³ The excitatory synapses of $M \sim S$ at the red and blue cells are assumed to be at half strength only for the linear approximations of their responses shown in Tables II and III.

Surprisingly little information is lost in computing and transmitting the violet and purple content in such a primitive way rather than with separate color cell channels. The black response is unaffected. Except for fewer nonlinear effects resulting from the violet and purple signals passing through fewer neurons, the white response is also unaffected if the $M \sim S$ input to the red and blue cells is reduced as discussed in the previous paragraph. The color cell responses are unaffected for the absorption orderings that do not have violet or purple content. The three orderings in Table II with violet or purple content are still distinguishable by the red and blue responses, depending on whether the red or blue cell, or neither, has a larger response. The red and blue response magnitudes even provide measures of the relative absorptions for these orderings, as shown in the approximations in Table II. The only loss of information is the location of L between M and S for the violet–purple ordering $M < L < S$.

As mentioned earlier, the transmission of violet and purple information through the red and blue channels is supported by empirical evidence. Although violet and purple are common color names, people can describe all colors in terms of red, green, blue, yellow, black, and white.^{25–27} These are the six RAM responses that are correlates of these perceptions. Experimental evidence shows red and blue are seen in short wavelength light, with less red than blue, and the shortest wavelengths appear to have the highest proportion of red.^{28,29} This is what the RAM predicts. Short wavelength light produces the violet–blue absorption order-

ing $L < M < S$. Table II shows this ordering elicits red and blue responses, with a smaller red response than blue. For the shortest wavelengths, the M and L absorptions are both small and the red and blue responses are nearly equal according to approximations of Table II. If a photostimulus produces an absorption M that is smaller than both S and L , the perceived color is a nonspectral color since no monochromatic photostimulus of any wavelength can produce such absorptions. Purple is the most common name for such nonspectral colors, which are also commonly described as combinations of red and blue.²⁶ This agrees with the RAM. Tables II and III show the RAM has red and blue responses when M is the smallest absorption. Unlike red, green, blue, and yellow, unique violet and unique purple are exceedingly difficult to pinpoint; they are virtually always seen with another color, which is always red or blue.²⁶ This is also consistent with the RAM responses. Tables II and III show the only unique color cell responses are red, green, blue, and yellow, and the absorption orderings that are commonly perceived as violet or purple elicit responses from both the RAM's red and blue cells. The fact that the RAM's red and blue channels are capable of carrying the violet and purple information and are the only RAM channels capable of doing so is consistent with all of these phenomena.

Chromaticity

Here it is shown that the RAM's color cells make chromatic color distinctions. The black and white cells make no contribution to these distinctions. What constitutes sufficiently different photostimuli to make a chromatic distinction is the same for the RAM as it is for actual perception.

The standard definition of chromatic color distinction is the ability to distinguish sufficiently different spectral distributions of light independently of intensity.^{20,30} Absorption ordering is independent of light intensity. By Tables II and III, this means the same combination of the RAM's output cells responds to a photostimulus of a given spectral distribution under any intensity. Suppose two photostimuli differ enough to produce different orderings of the three cone absorptions. If different color cells respond to the two orderings, no adjustment of intensity can force the same cells to respond to the two stimuli. The different combinations of color cell responses distinguish the two stimuli independently of intensity. That is, the color cells are able to make chromatic color distinctions by the definition above. According to Table II, three of the six orderings with strict inequalities have red and blue cell responses. In this case the orderings can still be distinguished independently of intensity by the relative magnitudes of the red and blue responses, although making the distinction may not be as easy as when different color cells respond.

What constitutes sufficiently different spectral distributions of light to make a distinction is also the same for the RAM as it is for actual perception. Two different orange colors can be difficult to distinguish under changes in intensity. If one appears to have less yellow than the other, increasing its intensity causes a Bezold-Brücke hue shift to

a yellower appearance. It will be shown that the RAM responses have changes that are identical to Bezold-Brücke hue shifts. If a photostimulus elicits red and yellow RAM responses, increasing the intensity of the stimulus causes the red cell response to decrease and the yellow cell response to increase.

Two spectral distributions of light are sufficiently different for the RAM to make chromatic color distinctions if they elicit different absorption orderings. The orderings are distinguished by the different combinations of color cell responses or, in the case of violet and purple orderings, by the relative magnitudes of the red and blue cell responses. It can be shown directly, but it is easier to see in the approximate RAM responses $\text{white} = \min\{S, M, L\}$ and $\text{black} = 1 - \max\{S, M, L\}$, that the black and white cells' responses are independent of the ordering of $S, M,$ and L . Therefore the black and white cells make no contribution to this chromatic color distinction.

Hue, Saturation, and Brightness

RAM correlates of hue, saturation, and brightness are defined here in terms of RAM responses. For any photostimulus, the RAM correlate of *color saturation* is the sum of the color cell responses. Using the approximations of Tables II and III, saturation is a number in the interval $[0, 1]$. Since the approximations also imply the sum of the RAM responses is approximately 1, saturation is approximately one minus the sum of the black and white responses. The sum of the black and white responses is a measure of how *desaturated* the color is. For the RAM saturation to be large, the total color cell response must be large, and both the black and white cell responses must be small. This corresponds to the perception of a highly saturated color having high color content and little or no black or white component. If either the black or white cell response is large, the RAM saturation is small. This corresponds to the perception that a color can be desaturated by either a black or white component.

The RAM correlate of the *brightness* or *lightness* of a photostimulus is the white cell's response minus the black cell's response. The term brightness is sometimes restricted to an apparent quality of luminous objects, and lightness is used to describe reflected light. This distinction is not made here since the RAM's brightness is defined simply for a photostimulus impinging on a few neighboring cells in the retina. Distinguishing between luminous objects and objects that reflect light likely requires spatial contrast. Since all neural responses are in the interval $[0, 1]$, brightness is a number in the interval $[-1, 1]$. The RAM brightness is 1 when the only response is white = 1, and RAM brightness is -1 when the only response is black = 1. These RAM extremes of brightness correspond to the perceived extremes of pure white at one end and black at the other. If the white response is not greater than the black response, the RAM correlate of *darkness* is defined as the magnitude of brightness. That is, $\text{darkness} = |\text{brightness}|$ if $\text{brightness} \leq 0$. Darkness is a number in the interval $[0, 1]$, with darkness = 0 when the black and white responses are equal, and

darkness = 1 when black = 1 is the only RAM response. Darkness is simply an alternative description of negative values of brightness. It will be shown that the RAM correlate of brightness explains the additivity failure of brightness.

If two color cells respond to a photostimulus, the RAM correlate of *hue* is the ratio of the smaller response to the larger. In this case, hue has a color name and $0 < \text{hue} \leq 1$. For example if the green response is 0.3 and the yellow response is 0.6, the green:yellow hue is 1:2. This is the RAM correlate of the perception of greenish-yellow, and the ratio one half is the correlate of the perception that the green content is half as strong as yellow. If the green and yellow cells have equal responses, the green:yellow hue or yellow:green hue is 1. If only one color cell responds, that color is defined to be the RAM correlate of hue. For example if the yellow cell is the only color cell to respond, the hue is yellow. If no color cell responds, the RAM correlate of hue is undefined.

If color is perceived as hue, saturation, and brightness, it may seem that each one should have a single neuron response as its correlate. Hue, saturation, and brightness, however, are not single perceptions. Each one is normally described as one or two perceptions for which the RAM has single neural correlates. Hues have many descriptive names such as orange and chartreuse, but they can be described as red, green, blue, or yellow, or as the relative strengths of two of these four colors. A color's saturation is described in terms of the strength of its apparent color content or in terms of its black or white content. The opposite of "bright" or "light" is usually described as "dark" rather than "not bright." These descriptions correlate with the relative strengths of the RAM's black and white cell responses.

Color Space

The set of approximate RAM responses is shown in Fig. 2. This shape and its geometric properties given here follow from the fact that the sum of the approximate RAM responses is 1. The figure consists of four tetrahedra, each with vertices labeled black, white, and two color names. The tetrahedra are joined at their common faces, and their edges are scaled to have length 1. Each tetrahedron is a subset of a four-dimensional space. This dimensional relation is an extension of the familiar concept of a one-dimensional line on a two-dimensional plane, or a two-dimensional triangle on the side of a three-dimensional pyramid. Figure 2 can be visualized since it is three-dimensional, but it is made up of points that have four coordinates because it exists in four-dimensional spaces. Each point in the figure lies in one or more of the four tetrahedra. The coordinates of the point are the four approximate RAM responses to a triple of receptor absorptions (S, M, L). Each RAM response is the distance from the point to the tetrahedron's face opposite the vertex that names the RAM response. The distance is measured along a line parallel to any edge.

For example, the point illustrated in Fig. 2 is approximately (red, blue, black, white) = (0.2, 0.4, 0.1, 0.3). The

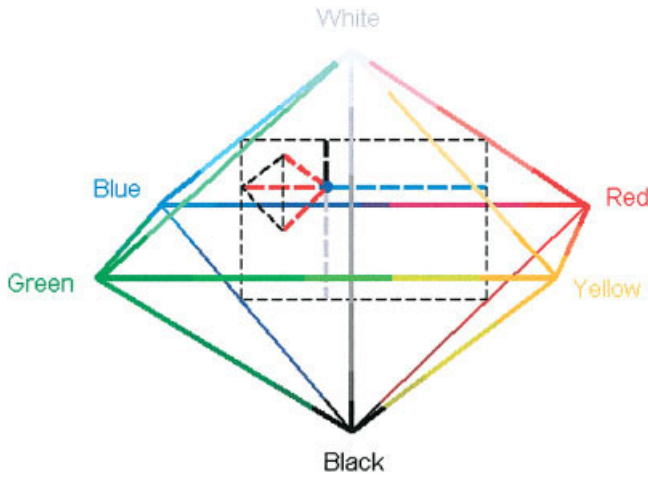


FIG. 2. Color space of the Relative Absorption Model. This three-dimensional figure in four-dimensional space represents the set of RAM responses. Each point in the figure lies in a tetrahedron with vertices labeled black, white, and two color names. The coordinates of the point are four RAM responses to three receptor absorption values. Each response is approximately the distance from the point to the tetrahedron's face opposite the vertex that names the response, with the distance measured along a line parallel to any edge. The point shown is (red, blue, black, white) = (0.2, 0.4, 0.1, 0.3).

coordinates are the lengths of the dashed line segments shown extending from the point to the tetrahedral faces. The red response 0.2 is shown in all three of the possible ways to the blue–black–white triangle along lines parallel to the edges that meet at the red vertex. The point is the approximate RAM response to the cone absorption $(S, M, L) = (0.9, 0.5, 0.3)$. The responses are computed according to the approximations for the violet–blue ordering given in Table II: the red response is $(S - M)/2 = (0.9 - 0.5)/2 = 0.2$, etc. The colors in Fig. 2 are meant to be suggestive of RAM responses, but a more accurate representation would show continuous color change along any path connecting two points. The assumption that the $M \sim S$ signal strength is halved affects only the region of the figure that has both red and blue responses. Without the assumption, that region would not be exactly tetrahedral but would still fit into the figure with faces at the red–black–white triangle and blue–black–white triangle.

The RAM's correlates of hue, saturation, and brightness are three-dimensional cylindrical coordinates for RAM color space. For any point in the space, its cylindrical coordinates are $r = \text{saturation}$, $\theta = \arctan(\text{hue})$, and $z = \text{brightness}$. The second coordinate can be expressed equivalently as $\text{hue} = \tan(\theta)$. If two color cells respond, then $0^\circ < \theta \leq 45^\circ$ since $0 < \text{hue} \leq 1$. For a yellow:green hue, for example, $\theta = \arctan(\text{yellow}:\text{green})$. The angle is rotated about the black–white line segment from the green vertex toward the yellow vertex. If only one color cell responds, θ is defined to be 0° . If no color cell responds, there is no hue and saturation is 0. This corresponds to the fact that in cylindrical coordinates θ can have any value if $r = 0$. The cylindrical coordinates transform the color space of Fig. 2

into the familiar spindle shape shown in Fig. 3. This is because the RAM's saturation defines a mathematical metric, or distance, from each point in Fig. 2 to the black–white line segment, and this metric is constant on each square cylinder centered on the black–white line segment. At each point in the black dashed rectangle in Fig. 2, for example, saturation is the sum of the red and blue cell responses, which is the length of the rectangle. Since the set of points equidistant from a line defines a circular cylinder, the saturation metric transforms the square cylinders of Fig. 2 into circular cylinders as depicted in Fig. 3. The spindle shape is determined by the restriction $r + |z| \leq 1$, which follows from the sum of the approximate RAM responses being 1. Figures 2 and 3 are topologically equivalent. They represent the same color space of RAM responses but with different coordinate systems.

The geometric properties of the cylindrical coordinates, illustrated in Fig. 3, are identical to the usual geometric descriptions of perceived hue, saturation, and brightness. On horizontal circles centered on the black–white axis, only hue varies while saturation and brightness are constant. Only brightness varies on vertical lines, and only saturation varies on radial lines perpendicular to the black–white axis. Hue is constant on vertical triangles that contain the black–white axis, brightness is constant on horizontal cross sections, and saturation is constant on circular cylinders about the black–white axis.

Three-dimensional figures similar to Figs. 2 and 3 have long been thought to be natural representations of color

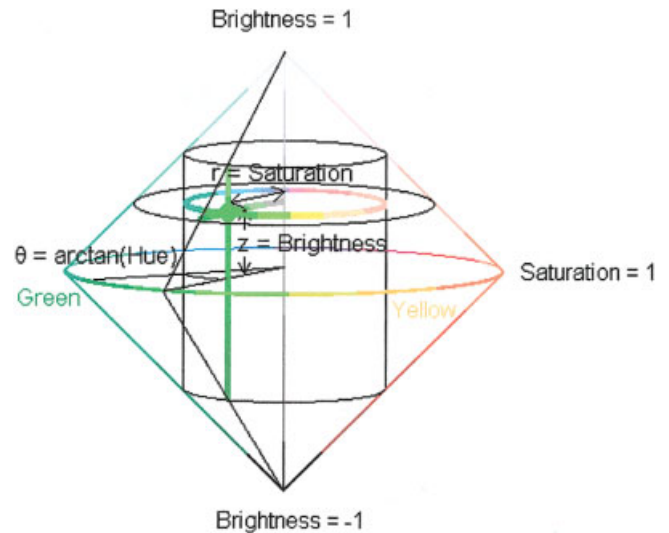


FIG. 3. Hue, saturation, and brightness. The customary spindle-shaped color space is determined by the RAM's hue, saturation, and brightness, which are cylindrical coordinates for the RAM color space of Fig. 2. At each point in the figure, saturation is the distance from the black–white axis, brightness is measured vertically from the middle horizontal cross section, and hue is the tangent of the angle of rotation from the nearest unique color response. The cylindrical coordinates of the point shown are approximately (saturation, brightness, yellow:green hue) = (0.5, 0.3, 0.25). The four-dimensional rectangular coordinates are (green, yellow, black, white) = (0.4, 0.1, 0.1, 0.4).

perception. The first such figure was Philipp Otto Runge's color sphere, with white at the north pole, black at the south, and hues on the equator.³¹ The best-known and most-used three-dimensional figure may be the "color tree" that the artist Albert Munsell constructed to mend "the incongruous and bizarre nature of our present color names."³² Depictions of color solids are most often spindle shaped as shown in Fig. 3, following the figure of Nobel laureate Wilhelm Ostwald.³³ The middle horizontal cross section of Fig. 3 is similar to the familiar color wheel first formulated by Isaac Newton.³⁴ Since Newton's colors became "diluted" with whiteness close to the center rather than with gray, his color wheel is actually topologically equivalent to the top surface of Fig. 3. The circular edge shown in Fig. 3 is the familiar color circle of saturated hues.

The RAM predicts an approximation of the RAM color space could be constructed simply by arranging colored chips so that adjacent chips appear as similar as possible, which is just what Munsell did. Colored chips with white components of various strengths can easily be arranged in a disk like Newton's color wheel, and saturated colors can easily be arranged in a circle similar to the circular edge of Fig. 3. The similarities of common color figures to Figs. 2 and 3 support the hypothesis that the RAM responses are neural correlates of color vision. Although arranging colored chips into the shape of the RAM's color space is a simple matter, it would be difficult to deduce from observable color phenomena that the resulting three-dimensional figure consists of subsets of four different four-dimensional spaces, what each quadruple of variables represents, what their values are, that their sum is approximately constant, and how the four dimensions of colors and black and white map into the three dimensions of hue, saturation, and brightness. These aspects of color space may be the source of some of the confusion about color. An understanding of the color properties in the geometry of color space could eliminate the confusion.

Other color spaces can be derived from the RAM color space. For example, if the amounts of imaginary, idealized red, green, and blue lights assumed for CIE space are taken as approximations of the cones' absorptions, CIE space can be produced by projecting the RAM color space preimage (the set of absorption triples that map into RAM color space) onto the "red-green" plane. Each point (S, M, L) projects onto $(L/(S + M + L), M/(S + M + L))$. The preimage, rather than simply the set of all possible absorption triples, is necessary so that the RAM's colors can be associated with the points in the plane. The difference between RAM color space and other color spaces is that RAM space is predictive and others are descriptive. CIE space and Munsell's color tree describe what colors people say they see. The RAM's explicit neural network explains how perceptions might be generated and provides numerical measures of the perceptions in terms of neuron responses.

Until now the geometry of color has not had an explanation based on an explicit neural structure. Even the seemingly mundane transformation of the visible spectrum from a linear interval of wavelengths of light to the perceptions of

hues on a closed curve is invariably presented in standard textbooks with no explanation or with the explicit assertion that there is no explanation. The RAM not only generates the familiar geometric representation, but also provides numerical measures for the points in the figure and gives meaning to the measures. The coordinates of each point are approximately the magnitudes of four neuron responses to a triple of receptor absorptions. Their values are the distances from the point to the four sides of the tetrahedron containing the point and are measures of color and black and white. These neural responses also provide measures of hue, saturation, and brightness, which are cylindrical coordinates of the figure. If the RAM responses are neural correlates of color vision, the set of RAM responses that make up the topologically equivalent Figs. 2 and 3 can rightfully be called color space.

The Continuous yet Categorical Nature of Color

While it is apparent there are categories of color (green, greenish-yellow, etc.), the categories seem to overlap and there appears to be a continuum of colors from one category to another. The realizable combinations of RAM color cell responses are correlates of the perceived color categories. A color cell response common to three of these combinations is the correlate of the perceived overlap in color categories. The overlaps in the combinations link them together in a closed loop: red and blue, blue, blue and green, green, green and yellow, yellow, yellow and red, red, red and blue. These overlapping combinations of RAM responses correspond to the overlapping categories of perceived colors. The continuity of the color cells' response intensities is the correlate of perceived color continuity.

The RAM's outputs actually have several forms of continuity. The RAM responses to sensory stimuli are compositions of individual cellular response functions according to the synaptic connections of Fig. 1. Since individual receptor and neural response intensities are continuous functions of their input intensities by property 11 of Table I, the composite RAM responses are continuous functions of photostimulus intensity. If, in addition, the three absorption curves are continuous functions of wavelength, then the RAM responses to monochromatic light are continuous functions of wavelength. Because the receptors' absorption curves overlap, not all absorption triples (S, M, L) are realizable. For instance, $(0, 0, 1)$ cannot be achieved because any photostimulus that has a substantial absorption L also has a positive M . This means the set of realizable RAM responses may be a proper subset of the color space in Fig. 2. Because of the nonlinearities in neural responses, this subset may be nearly the whole color space. The triple $(S, M, L) = (0.1, 0.1, 0.9)$ may produce a red cell response nearly equal to 1, with almost no black or white cell response. If the set of realizable absorption triples is a connected set, then continuity of cellular responses implies the set of realizable RAM responses is a connected subset of the RAM color space. Connectivity means any two points in this subspace can be connected by a continuous path con-

tained in the subspace. Along any such path connecting two points, the six RAM responses change continuously. This property is the RAM correlate of the apparent continuum of colors.

Color Pairs

No color is described in any language as reddish-green or bluish-yellow. These mutually exclusive color pairs were the impetus for the historic debate over the trichromatic and opponent theories. Tables II and III show these two pairs are also mutually exclusive RAM color cell responses. No photostimulus causes both the red and green cells to respond or both the blue and yellow cells to respond. The RAM's explanation of mutually exclusive color pairs is different from the opponent theory's supposition that each color pair is transmitted through one neural channel in opposing kinds of signals. Simply put, except for the $M \sim S$ input to the red and blue cells that causes both of them to respond to violet and purple absorption orderings, the red cell responds if L is the largest absorption and green responds if M is largest. These absorptions cannot both be largest. The blue cell responds if L is smallest and yellow responds if S is smallest, and they cannot both be smallest. Tables II and III show the RAM color cells that can respond together are the same as the color pairs that can be perceived together. The RAM correctly predicts black and white are not mutually exclusive and can exist with any of the color combinations.

Color Mixing

A common observation that has played a central role in the history of color theory is that mixing colors can produce entirely different colors. Red light superimposed on green light is perceived as yellow, and yellow on blue appears white. The RAM produces these phenomena. A photostimulus that is perceived as red elicits a high L absorption and low S and M absorptions. This photostimulus elicits a high RAM red cell response by the approximations of Table II. A photostimulus that is perceived as green elicits a high M absorption and low S and L absorptions, and it has a high RAM green cell response. A mixture of the two stimuli must produce high M and L absorptions and a low S absorption. This stimulus has a high RAM yellow cell response. Similarly, a yellow photostimulus with high M and L values superimposed on a blue photostimulus with a high S value produces all high absorptions and has a high RAM white cell response.

Bezold-Brücke Hue Shift

Some colors appear to vary with the intensity of the photostimulus. Both orange and greenish-yellow appear yellower at higher intensities. Violet and greenish-blue appear bluer. These phenomena are known as Bezold-Brücke hue shifts.³⁵⁻³⁷ The RAM produces the phenomena, which follow immediately from two RAM properties. First, photostimulus intensity does not affect which color cells respond.

This property follows from the fact that photostimulus intensity does not affect absorption order. Second, except for the violet-purple and red-purple absorption orderings, if two color cells have significant responses at some photostimulus intensity, the blue or yellow cell has significantly greater response at higher intensities than the red or green cell. (For the violet-purple and red-purple orderings, the red response is at least as great as the blue response at all intensities.) The proof of the second property depends on the fact that as photostimulus intensity increases, the cones approach full saturation in the order of their absorptions. For example if $S < M < L$, the response ordering is $L < M < S$ and the RAM's red and yellow cells respond. As photostimulus intensity increases, L approaches zero first and the large difference between L and M produces a large red cell response. As intensity increases further, M approaches zero next, decreasing the red response and increasing the yellow response. This is the RAM correlate of a yellower orange. As before, "increasing" and "decreasing" refer to the fact that stimulus and response intensities are variables. They are not increasing and decreasing with time.

Additivity Failure

When two photostimuli are superimposed, the perceived brightness is not additive if the stimuli have sufficiently different spectral distributions. If a subject adjusts red and green fields to match the apparent brightness of a white field and the intensity of the white field is then doubled while the red and green are superimposed, the white field appears to be significantly brighter than the red-green mix (which is perceived as yellow or white).³⁸⁻⁴⁰ This phenomenon is known as the additivity failure of brightness. It is not due to nonlinearities in neural responses. If the white field and the red-green mix are viewed through a filter that absorbs half the light from each, restoring the white field to its original intensity, the white field still appears to be much brighter than the red-green mix.

The RAM explains the additivity failure of brightness. A white photostimulus has nearly equal absorptions $S \approx M \approx L$. Doubling the intensity of the white light doubles the absorption in each cone. If the cones were not already near full saturation, this doubling significantly increases the white cell response and significantly decreases the black response by the approximations of Table II. Since brightness is white - black, brightness is significantly increased. A red photostimulus is absorbed mainly by the L cone and much less by the M cone. The S cone absorption is negligible. Similarly, green light is absorbed mainly by the M cone and much less by the S and L cones. Superimposing red and green lights increases the absorptions $\max\{S, L, M\}$ and $\min\{S, L, M\}$ only slightly over the maximum and minimum absorptions of the separate red and green fields. Since the mixture has little effect on the black and white cell responses by the approximations of Table II, the brightness of the red-green mixture is also little changed from the brightness of the separate red and green fields.

Opponent-Color Cells

Neurons are seldom completely at rest. Even with no excitatory input, a typical neuron fires randomly at a low average rate. Greater inhibitory than excitatory input can hyperpolarize a cell, suppressing the output signal below the normal background rate. The resulting change in response can be measured directly in individual neurons. Some neurons, including retinal neurons, are activated by a photostimulus of one color and are suppressed by its mutually exclusive color. Considerable research has concentrated on these cells.^{9,41–46} They are referred to as opponent-color cells and have been taken as evidence supporting Hering's opponent theory, which supposes each mutually exclusive color pair is transmitted through one neural channel encoded in opposing kinds of signals.

The RAM has a different explanation of opponent-color cells. To illustrate the argument, the RAM's green cell is shown here to have green+red- opponency, meaning it is activated by green light and suppressed by red light. Middle wavelength photostimuli normally called green produce a large M absorption. The RAM's green cell responds to such photostimuli. For a long wavelength red photostimulus, the absorption ordering is $S < M < L$ and the response ordering is $L < M < S$. By property 4 of Table I, $S \sim M < S \sim L$. The green cell response is $(S \sim M) \sim (S \sim L)$. Since the green cell has greater inhibitory input than excitatory input, the output is suppressed. This shows the green cell has green+red-opponency. The green cell is neither activated nor suppressed by short wavelength photostimuli. At these wavelengths, $L < M < S$, $S < M < L$, and the green response is $(S \sim M) \sim (S \sim L) = 0 \sim 0$ by property 2 of Table I. By similar arguments the RAM's red cell has red+green- opponency, and it is also activated by short-wavelength light. The yellow cell has yellow+blue- opponency, and the blue cell has blue+yellow- opponency.

SUMMARY AND CONCLUSION

The RAM is a simple and explicit neural network that may resolve the question of how synaptic connections are organized to process spectral information. It receives input from three classes of spatially proximate photoreceptors, and its six outputs are neural correlates of color vision. The four color cells' responses, labeled red, green, blue, and yellow, are correlates of perceived colors. They identify which cones have the largest and smallest absorptions of photons and measure their differences from the middle absorption. Violet and purple information is transmitted through the red and blue channels, the only channels in the network that can accomplish this without a considerable loss of information. The white cell's response measures the smallest absorption and is the neural correlate of the perception of whiteness. The black cell's response measures how far the largest absorption is from full saturation and is the correlate of the perception of blackness. The RAM correlates of hue, saturation, and brightness agree with the usual descriptions of these perceptions. The color cells make chromatic color

distinctions that match actual perceptions. The black and white cells' responses are achromatic because they are independent of the absorption ordering. The RAM's responses make up a three-dimensional color space that provides quantitative neural explanations of standard color figures such as Newton's color wheel and Munsell's color system. The RAM generates color and related neural phenomena, including the continuous yet categorical nature of color, mutually exclusive colors and colors that can be perceived together, color mixing, the Bezold-Brücke hue shift, the additivity failure of brightness, and opponent-color cells. Although most of the color phenomena produced by the RAM are a familiar part of everyday experience and have generated enormous interest and speculation for thousands of years, they have not previously had explanations based on an explicit neural structure.

ACKNOWLEDGMENTS

The author thanks John Culliney, Howard Gillary, Anna Yoder Higashi, Robert Knighton, Jes Stollberg, Frank Tillman, Dan Yoder, Sheila Yoder, and the referees for reading the manuscript and providing many helpful suggestions.

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