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Mini Review

Seeing Color by Subtraction

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Abstract

Human color vision requires three types of cone photoreceptor cells (red, green and blue cones) located in the retina that absorb different wavelengths of visible light. The red, green, and blue cones each absorb electromagnetic radiation with long (600 - 700 nm), medium (500 - 600 nm) and short (400 - 500 nm) wavelengths, respectively. Light absorption by each type of cone cell causes a reduction in its outgoing electrical current that is detected in the visual cortex during color perception. In the absence of visible light, each cone cell sends a maximal electrical output (called dark current) to the visual cortex, which gives the sensation of black. By contrast, white light excites each cone cell equally, which greatly diminishes the electrical output from each cone and causes the sensation of white. The color red is perceived in the visual cortex when visible light (at 650 nm) enters the eye and is absorbed by the red cone. The red-light activation reduces the outgoing electrical output of the red cone while permitting maximal output from both the green and blue cones. This mini-review describes how color perception may be caused by a light-activated and wavelength-dependent attenuation of electrical output from each cone cell. We suggest that color is perceived in the brain by subtraction. For example, red is sensed when incoming light stimulation reduces the electrical output from the red cone (while the green and blue cones retain maximal output); yellow is sensed when light stimulation reduces output from both red and green cones (while the blue cone retains maximal output); and brown is sensed when the light reduces the outputs from the red, green and blue cones by 78%, 50% and 25%, respectively..

Keywords: *Cone Cell; Photoreceptor; Retina; Phototransduction; Cone Opsin; Color Vision*

Abbreviations

cGMP: Cyclic Guanosine Monophosphate; Na^+: Sodium Ion; opsin*: Light-Excited Cone Opsin; PDE: Phosphodiesterase; T: Transducin; T*: Light Activated Form of Transducin

Introduction

Cone photoreceptor cells in the vertebrate retina are essential for color vision [1,2]. The human retina contains three types of cone photoreceptors: red, green, and blue cone cells that each absorb electromagnetic radiation at long (600 - 700 nm), medium (500 - 600 nm) and short (400 - 500 nm) wavelengths, respectively. A schematic view of a cone cell is shown in figure 1A and 1B. The light-sensing region, known as the outer segment, contains stacks of disk membranes that are enriched with the light-absorbing visual pigment, cone opsin [3]. Human red cone opsin absorbs visible light maximally at ~600 nm (Figure 1C). Human cone opsins from green and blue cones absorb maximally at 530 and 425 nm, respectively [1]. Light absorption by the retinal chromophore in cone opsin (Figure 1B, red wave) promotes a protein conformational change, resulting in a metastable light activated state of the cone pigment [4,5]. The light-excited cone opsin (opsin* in figure 1B) activates a heterotrimeric G-protein (transducin) that in turn activates the enzyme phosphodiesterase (PDE), leading to a light-induced decrease in cGMP concentration [4,6,7]. An important consequence of the light-induced decrease in cGMP levels is that it causes cyclic-nucleotide gated ion channels in the plasma membrane to close (Figure 1B, lower inset), because these channels are kept open by the binding of cGMP in the dark (Figure 1A, lower inset) [8,9]. The opening of cGMP-gated ion channels in the dark-adapted cone cell causes a membrane depolarization that promotes a persistent electrical output (dark current) from the presynaptic bulb (Figure 1A) [10]. By contrast, light activation of the cone cell causes hyperpolarization of the plasma membrane that in turn leads to a diminution of electrical output (Figure 1B and 1D) [10-12]. At saturating levels of light stimulation, the electrical output from the cone cell is diminished by more than 100-fold (Figure 1D) [12]. In essence, light activation of a cone cell causes its electrical output to be turned off, in contrast to the maximal output that occurs in the absence of light.

The light-induced decrease in electrical output from a cone photoreceptor (Figure 1) suggests that color perception in the brain is a subtractive process. Dark-adapted cone cells (red, green and blue cones) each send a maximal electrical output (dark current) to the visual cortex that is perceived as black. By contrast, white light illumination (that contains all wavelengths from 400 - 700 nm) excites each cone cell maximally and equally, which abolishes the current output from each photoreceptor to cause the sensation of white. Color is perceived when the three types of cone cells are unequally turned off by light. For example, long wavelength light (650 nm) is perceived red because it turns off the red cone, without affecting the electrical output of the green and blue cones. Therefore, we suggest that color is perceived in the brain by a subtraction process. This mini-review describes how color perception may be caused by a light-activated and wavelength-dependent attenuation of electrical output from each cone cell that is processed in the visual cortex during color perception.

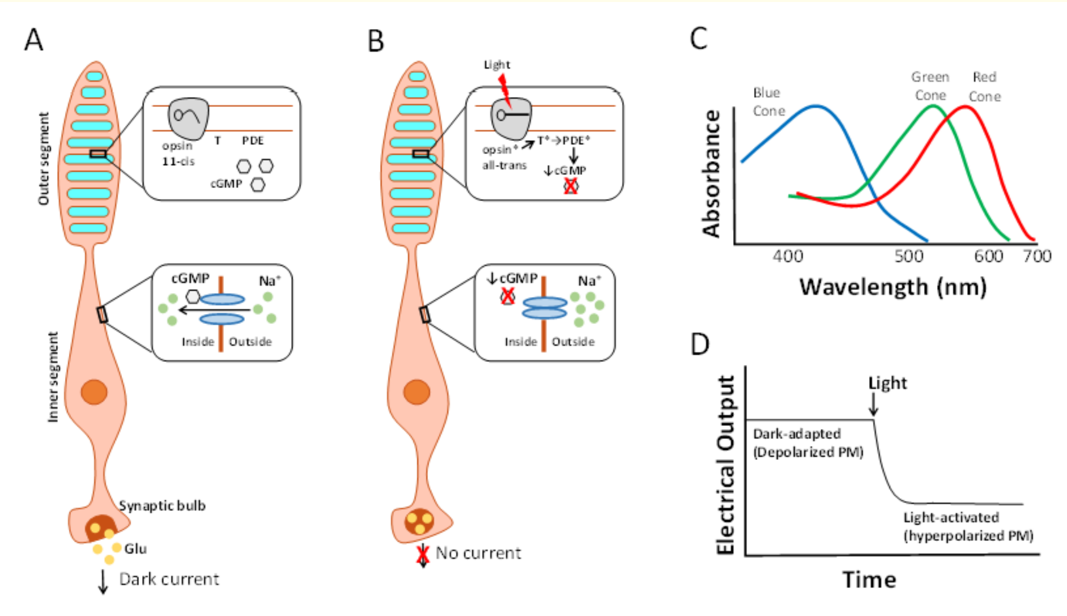

Figure 1: *Light activation of a cone photoreceptor cell. (A) Dark-adapted cone photoreceptor cell. Disk membranes containing cone opsin are cyan. An expanded view of a disk membrane is shown in the upper inset. Dark-adapted cone opsin has 11-cis retinal and phosphodiesterase enzyme (PDE) is inactive, allowing high levels of cGMP (hexagon) to accumulate in the dark. cGMP-gated ion channels (blue ovals) are kept open by the binding of cGMP in the dark-adapted cone (lower inset). The neurotransmitter, glutamate (yellow circles) is continually released from the synaptic bulb in the dark, giving rise to a dark current that is routed to the visual cortex. (B) Light-activated cone photoreceptor cell. Light absorption (red wave) by cone opsin causes photoisomerization of the retinal chromophore (11-cis to all-trans). Light-excited cone opsin (opsin*) activates transducin (T*) that in turn activates phosphodiesterase (PDE*), causing hydrolysis of cGMP (upper inset). The light-induced decrease in cGMP levels causes ion channels in the plasma membrane to close (lower inset). Light activation of the cone cell shuts off the release of neurotransmitter from the synaptic bulb. (C) Visible light absorption spectra of the three human opsin cone pigments. (D) Electrical output from a cone photoreceptor. Dark-adapted cones have a depolarized plasma membrane (PM) with a large dark-current. Light-activated cones have a hyperpolarized plasma membrane that causes reduced electrical output.*

Discussion

A schematic model that simulates subtractive color perception is shown in figure 2. A central feature of our model is that the three types of cone photoreceptors (red, green, and blue cones) each send a maximal output to the visual cortex in the absence of visible light (designated by arrows in figure 2). We postulate that the electrical output from the red, green and blue cones each code for the perception of cyan, magenta and yellow, respectively, in the visual cortex. We propose that black is perceived as a composite of cyan, magenta and yellow signals detected in the visual cortex in the absence of light (Figure 2A). In other words, the maximal outputs from each dark-adapted cone photoreceptor (cyan, magenta and yellow) are combined in the visual cortex to form the sensation of black (black=cyan+magenta+yellow). This concept of black is analogous to the black that is formed when mixing equal amounts of the printing inks that are colored cyan, magenta and yellow. The visual perception of black is illustrated in figure 2A and simulated in the video (https://youtu.be/AejejsJaZ10).

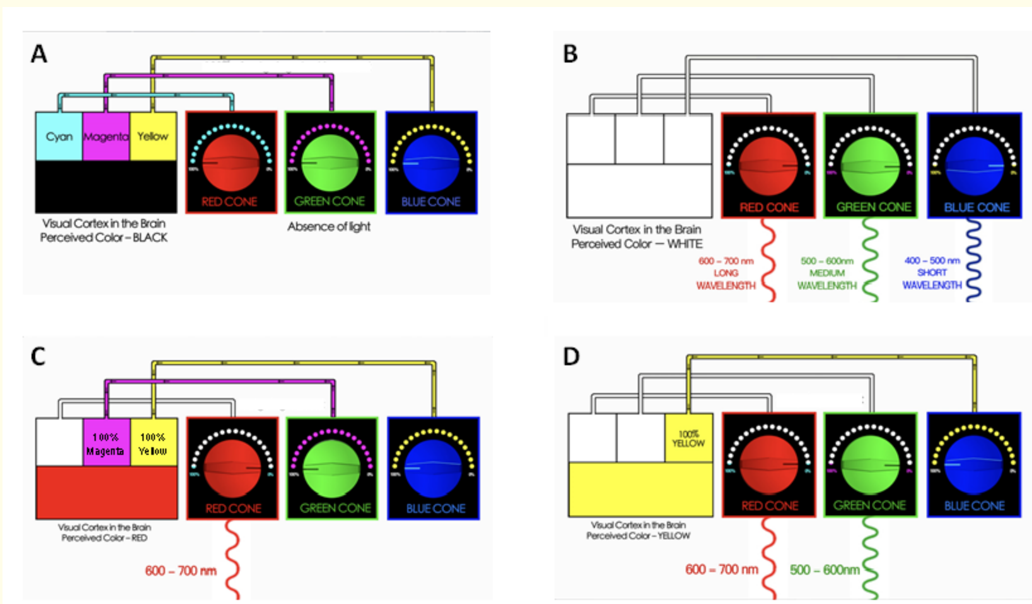

Figure 2: *Schematic model of subtractive color perception. (A) Perception of black in the absence of incoming light. The red, green and blue photoreceptor cone cells are depicted by black boxes that contain red, green and blue dials. The electrical output from each photoreceptor is depicted by arrows. Outputs from red, green and blue photoreceptor cells are separately mapped to the visual cortex and perceived as cyan, magenta and yellow, respectively. In the absence of light, the maximal and equal electrical output from each photoreceptor cell are combined in the visual cortex to give the sensation of black (black = cyan+magenta+yellow). (B) Perception of white in the presence of incoming white light (represented as red, green and blue waves). White light absorbed equally by the red, green and blue cones abolishes the electrical output from each photoreceptor. This light-induced attenuation of output eliminates any cyan, magenta and yellow perception in the visual cortex and produces a white sensation (white box in visual cortex). (C) Perception of red in the presence of 650-nm light. The 650-nm light (red wave) is absorbed by the red cone cell, which attenuates its electrical output. The 650-nm light is not absorbed by the green and blue cones, which allows their output (magenta and yellow) to be combined in the cortex to give the sensation of red (red=magenta+yellow). (D) Perception of yellow in the presence of red and green light. Red and green light (red and green waves) are absorbed by red and green cones, which abolishes their output. The unexcited blue cone sends its output (yellow) to the visual cortex, which gives the sensation of yellow.*

The subtractive model also explains the perception of white light (Figure 2B). White light illumination is a form of electromagnetic radiation that contains a collection of wavelengths from 400-700 nm, which uniformly excite all three types of cone photoreceptors (red, green, and blue cones). This uniform light activation causes the electrical output from each cone cell to be markedly reduced (Figure 1D). Thus, the white light activation causes a uniform reduction of electrical output from each photoreceptor that is then sent to the visual cortex where it is perceived as white. In other words, the white light illumination subtracts the perception of cyan, magenta and yellow hues in the visual cortex, and the absence of photoreceptor output to the cortex is postulated here to represent white. This perception of white is illustrated in figure 2B and in the video (https://youtu.be/QYOV3sJ8KHA).

Let's now consider how the subtractive model explains the perception of red light (Figure 2C). A monochromatic form of visible light at 650 nm that enters the eye will activate red cone cells in the retina (without activating the green and blue cones) and cause the electrical output of the red cone to be reduced, while the electrical outputs from the green and blue cones remain maximal. The light-induced decrease in output from the red cone causes a subtraction (or removal) of cyan perception in the visual cortex, while the perception of magenta and yellow signals (provided from the green and blue cones) remain intact. In essence, the 650-nm light is perceived as red because it subtracts the perception of cyan, while retaining the combined perception of magenta and yellow (red=magenta+yellow). The visual perception of red light is illustrated in figure 2C and simulated in the video (https://youtu.be/QNLsRxRsPO0).

Lastly, the subtractive model explains how the mixing of red and green light produces a yellow sensation (Figure 2D). It seems non-intuitive that mixing red and green would produce yellow. Indeed, equal mixing of red and green paint does not produce a yellow paint mixture. So, why is it that red light and green light combine to make yellow? According to our subtractive model below (Figure 2D), an equal mixture of red and green light that enters the eye will excite the red and green cones equally, while the blue cone will remain unexcited. The red-light activation reduces the red cone output (which subtracts cyan from the cortex), while the green-light activation reduces the green cone output and subtracts magenta. As a result, the red and green light subtract both cyan and magenta from the cortex, but the unexcited blue cone continues to provide output that codes for yellow. In essence, the red and green light are subtracting cyan and magenta from the cortex, while leaving intact the perception of yellow. The visual perception of yellow caused by mixing red and green light is illustrated in figure 2D and simulated in the video (https://youtu.be/_poOLz6SdZg).

Conclusion

We present a subtractive model of color perception that can accurately simulate the perception of any color caused by arbitrary light stimulation of the three cone photoreceptors (Figure 2 and https://www.youtube.com/watch?v=i6JQSQphyu4). A key feature of our model is that color is perceived by subtraction. For example, 650-nm light is perceived red because it reduces electrical output from the red cone cell (i.e. subtracts cyan from the cortex), while permitting output from the green and blue cones that code for the perception of magenta and yellow (red=magenta+yellow). Red and green light is perceived as yellow because red light reduces the red cone cell output (subtracts cyan) and green light reduces the green cone cell output (subtracts magenta), while permitting output from the unexcited blue cone that codes for yellow. The perception of more complex colors, like brown, can be simulated by differentially activating the three cone photoreceptors. For example, brown = 78% red light (22% cyan in the cortex) + 50% green light (50% magenta in the cortex) + 25% blue light (75% yellow in the cortex). A simulation of the visual perception of brown can be found at https://youtu.be/NCX543N_d_8.

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