



Review article

Chromatic clocks: Color opponency in non-image-forming visual function

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ABSTRACT

During dusk and dawn, the ambient illumination undergoes drastic changes in irradiance (or intensity) and spectrum (or color). While the former is a well-studied factor in synchronizing behavior and physiology to the earth's 24-h rotation, color sensitivity in the regulation of circadian rhythms has not been systematically studied. Drawing on the concept of color opponency, a well-known property of image-forming vision in many vertebrates (including humans), we consider how the spectral shifts during twilight are encoded by a color-opponent sensory system for non-image-forming (NIF) visual functions, including phase shifting and melatonin suppression. We review electrophysiological evidence for color sensitivity in the pineal/parietal organs of fish, amphibians and reptiles, color coding in neurons in the circadian pacemaker in mice as well as sporadic evidence for color sensitivity in NIF visual functions in birds and mammals. Together, these studies suggest that color opponency may be an important modulator of light-driven physiological and behavioral responses.

1. Introduction

Virtually all organisms modulate their behavior and physiology (including rest-activity cycles, feeding, metabolism, immune function, hormone secretion, and cognition) according to time of day, as defined by the Earth's axial rotation. Critical components of this modulation are the sensory input pathways that entrain internal biological clocks to external time. The German word *zeitgeber* ("time giver") is used to refer to diurnal cues in the environment that are detected by these pathways and thus act to synchronize endogenous circadian rhythms to external time. Circadian rhythms persist in the absence of zeitgebers, but run at their own intrinsic period that is typically either slightly shorter or longer than 24 h (Wever, 1979). While temperature (e.g. Pittendrigh, 1960; Sweeney and Hastings, 1960), food availability (e.g. Brinkhof et al., 1998), and social interactions (e.g. Ehlers et al., 1988) can reset the circadian clock, light remains the best-studied and, under most circumstances, the most influential zeitgeber.

Studies of circadian photosensitivity have largely investigated the role of changes in light intensity, which is the more prominent diurnal characteristic of environmental illumination. Recent findings suggest that this is only one part of the picture: In mice, changes in the color of the ambient light can contribute to entraining circadian rhythms (Walmsley et al., 2015). This is accomplished using *color opponency* in which the signals from two different photoreceptor classes with different spectral tuning are subtracted, thereby encoding changes in

the relative wavelength content of the light that occur during dusk and dawn.

While systematic comparative surveys of color sensitivity for image-forming-vision (e.g. Menzel (1979) for invertebrates, and Jacobs (1993) for mammals) show that color vision is extremely widespread, few investigators have examined color sensitivity for circadian regulation. That color opponency can be used to provide a marker of twilight for circadian entrainment has been suggested previously (Donley, 1975; Ekström and Meissl, 2010; Fleissner and Fleissner, 2002; Korf et al., 1981; Morita et al., 1987b; Roenneberg and Foster, 1997; Solessio and Engbreton, 1993). As discussed below, color opponency appears to be a pervasive feature of the sensory systems involved in non-image-forming (NIF) visual functions in many organisms, indicating that it may be a key adaptation to the signals available from the photic environment predictive of important diurnal events such as the timing of twilight.

Here, we synthesize disparate sources of evidence indicating that systems for measuring color may be a conserved component of the photic input pathways controlling circadian clocks across the animal kingdom. As a departure point, we will describe the changes in the intensity and color of natural illumination taking place throughout the day (Section 2). We will then consider how these changes could be encoded, and describe in detail the properties of a color opponent system (Section 3). Next, we will turn to organisms employing a color-opponent encode to regulate their diurnal behavior, or having color-

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opponent circuitry in organs thought to be involved in it, spanning fish, amphibians, reptiles, and birds, and point out that wavelength-specific opponent behavior already exists in unicellular organisms (Section 4). We will then review evidence for color coding in the photic control of the mammalian circadian system and consider in particular sensitivity to color in human circadian rhythms (Section 5). Finally, we consider future directions for studying color sensitivity in NIF visual functions in humans (Section 6).

2. The photic environment: light-dark cycles and spectral dynamics of twilight

As the Earth rotates around its own axis, the ambient light undergoes predictable changes in intensity and spectrum as a function of solar angle. During the day, the ambient light is 1,000,000 to 100,000,000 times brighter than at night. On a clear night, starlight provides an illuminance of about ~ 0.001 lx, while moonlight is about ~ 0.2 lx; by comparison, sunlight may reach up to 100,000 lx. The ambient light intensity at a given point during the day depends on the atmospheric conditions and may vary at fine time scales due to cloud cover and atmospheric turbidity. In addition, light availability will also fluctuate substantially as organisms move in and out of shaded areas (Peirson et al., 2009).

The ambient light intensity changes systematically around twilight (Daan and Aschoff, 1975; Kern, 1992): The intensity decreases (at dusk) or increases (at dawn) as a function of solar elevation angle relative to the observer (Fig. 1a, b). After the sun has set below the horizon during twilight ($\theta_s < 0^\circ$) and no provides direct illumination, the light in the sky results from refraction and scattering of sunlight in the upper atmosphere, providing nonetheless moderate illumination. Twilight can be separated into three distinct phases by solar angle and the prevailing visibility conditions due to the illumination level (Fig. 1a, b): *Civil twilight* ($-6^\circ < \theta_s < 0^\circ$), when terrestrial objects can be identified and distinguished, *nautical twilight* ($-12^\circ < \theta_s < -6^\circ$), when only the outlines of objects are visible, and *astronomical twilight* ($-18^\circ < \theta_s < -12^\circ$), when the illumination is dark enough such that stars and other astronomical objects can be seen in the sky (United States Naval Observatory Astronomical Applications Department, 2005).

During twilight, not only the intensity of the illumination changes, but also the spectral composition and apparent color (Fig. 1c), giving rise to colorful phenomena visible to the human eye at dusk and dawn such as the yellow arches during civil twilight, and the purple-red sky during nautical twilight (Lee, 1994; Lee and Hernandez-Andres, 2003; Lynch and Livingston, 2001). A typical twilight spectrum is blue shifted compared to the daylight spectrum (Le Grand, 1968), with peak power at around 455 nm (Fig. 1c; McFarland and Munz, 1976; Palmer and

Johnsen, 2014; Spitschan et al., 2016; Sweeney et al., 2011; Walmsley et al., 2015). These spectral shifts are robust as a function of lunar phase until the sun has set 8° below the horizon (Palmer and Johnsen, 2014).

3. Resetting the circadian clock with color

3.1. Encoding ‘color’

Changes in the spectral composition of the ambient light are predictive of the onset of dawn and dusk. However, a single photopigment or photoreceptor class is unable to track changes in spectral composition and dissociate them from the changes in intensity which occur concurrently around dawn and dusk. This is a direct consequence of the *principle of univariance* formulated by Rushton (1972): A single photopigment class cannot distinguish between a change in intensity at a given wavelength and a change in wavelength at a given intensity. In other words, individual photopigments are “color blind”, as the generated output signal could be elicited by many different relative spectra of appropriately adjusted intensity, or in the more trivial case, two monochromatic lights of different wavelengths to which the photopigment is equally sensitive. To detect changes in spectral composition unambiguously, it is therefore necessary to compare the activity of two photopigments against each other. In such a color opponent system, outputs from different photopigments are subtracted from one another, such that stimulation by some narrowband wavelengths yields an excitatory response, while other wavelengths yield an inhibitory response. This enables a color opponent system to encode changes in the spectral composition of a spectrally complex light (such as daylight) (Fig. 2).

One potential advantage of using a color opponent code to track twilight (Fig. 2) is that differencing signals from two photoreceptors eliminates shared noise (Buchsbbaum and Gottschalk, 1983): A subtraction operation between two signals corrupted by the same noise (e.g. a variation in overall intensity of the signal) will remove the noise, a procedure termed common-mode noise rejection in engineering contexts. Such shared noise could arise from intensity fluctuations due to cloud cover or ‘behavioral noise’ introduced by moving between shaded and unshaded areas (Peirson et al., 2009). In turn, opponency effectively removes information that is common to both photoreceptors, thus reducing redundancy and maximizing information transmission (Atick et al., 1992; Buchsbbaum and Gottschalk, 1983; Lee et al., 2002).

3.2. Color opponent codes in image-forming vision

Color opponent coding is well documented in the visual systems of many different species and in many visual structures associated with

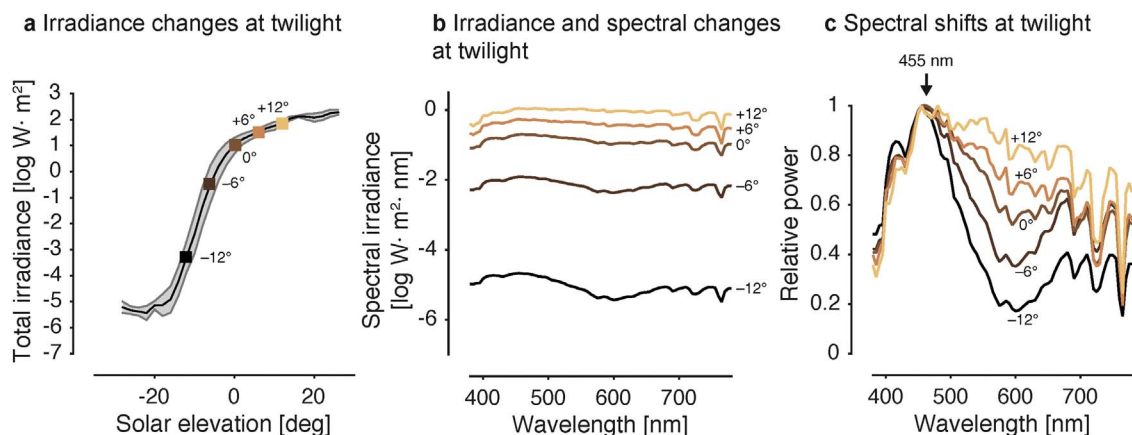


Fig. 1. Changes in the photic environment at twilight. a. Changes in irradiance as a function of solar elevation. Key points are emphasized by square markers. b. Changes in irradiance and spectrum at twilight on logarithmic axis. Color coding of single lines follows colors of markers in panel a. c. Changes in spectrum (normalized to 455 nm), showing relative short-wavelength enhancement during twilight. Data from Spitschan et al. (2016).

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