Chapter

Circadian Sensation and Visual Perception

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Abstract

The physiology of living beings presents oscillations that are known as biological rhythms. The most studied rhythm is called circadian (circa = circa, dies = day), because it varies with a period close to 24h. Most functions of the body have circadian variations, one can mention, for example, metabolism, body temperature, the activity of the nervous system, secretion of hormones such as melatonin and cortisol. Circadian rhythms were also found in human behavior, for example: in sensory activity, motor activity, reaction time, visual perception, auditory perception, time perception, attention, memory, arithmetic calculus, and executive functions. The present work reviews the visual path that participates in the synchronization of circadian rhythms, as well as the evidence that exists about the presence of circadian rhythms in the sensation and visual perception of the human being.

Keywords: circadian rhythms, sensation, visual perception

1. Introduction

1.1 Circadian rhythms

Circadian rhythms have several characteristics that are important to analyze. Under constant environmental conditions, these rhythms persist in a period close to 24 h. However, some of the physiological functions have different periods, so that circadian rhythm are considered as part of a multioscillative system [1]. However, the circadian rhythms of the different functions remain synchronized by a central pacemaker, located in the suprachiasmatic nucleus of the hypothalamus [2]. A set of genes involved in the generation and modulation of these rhythms was verified [3]. It was found that some environmental events keep circadian rhythms synchronized with environmental cycles. These synchronization agents are lighting cycles, room temperature, food availability, exercise, and social stimulation. Ambient lighting cycles are the most effective synchronize circadian rhythm, both in animals and in humans [4].

Three neurophysiological pathways participate in the responses of humans to light. The first clue includes two types of receptors in the retina, rods and cones, which respond to the intensity and frequency of light. These receptors are connected with bipolar and amharic cells, and ganglion cells that connect to neurons in the lateral geniculate nucleus of the thalamus and neurons in the occipital cortex. This nervous

path participates in the analysis of shapes, colors, and images. The second pathway involves ganglion cells in visual connections with nuclei of the superior colliculus of the thalamus midbrain, pulvinar nuclei, and the inferior temporal cortex. This nervous path participates in the identification of space. The third visual pathway includes a group of retinal ganglion cells that respond to light, have connections to the suprachiasmatic nucleus and participate in the mechanism of synchronization of circadian rhythms. These retinal neurons are known as intrinsically photosensitive retinal ganglion cells (ipRGCs), retinal ganglion cells give photosensitive (CGRP), or retinal ganglion cells that contain melanopsin (mRGCs) [5, 6].

2. Visual pathway that participates in the synchronization of circadian rhythms

Photosensitive ganglion cells are located in greater quantity in the center of the retina with a decrease towards the periphery, their axons protrude into the suprachiasmatic nucleus and other subcortical visual areas involved in the entrainment of light Dacey et al. [7]. It is important to note that only 3% of the total ganglion cell population is photosensitive. Morphologically ipRGCs present large receptive fields and their depolarization (inverse process of rod neurons and hyperpolarized cones) happens in dendrites and axons. They can be classified into five cell subtypes [8]: cells type M1 (have higher neuronal density and higher levels of opsin expression), cells type M2 and M3, (have levels of expression of medium opsin), and cells of type M4 and M5 (have low levels of expression of opsin). Ecker et al. [9] showed that M2 and M4 cells send neural information to various regions of the brain, including areas involved in visual processing through dorsal and ventral areas of the lateral geniculate nucleus of the hypothalamus.

The dendrites of ipRGCs receive photoreceptor inputs (cones and rods) via bipolar and amharic cell connections [10]. These findings hypothesized that ipRGC cells relay luminosity-sensitive visual input signals in sustained circadian time. Since these pathways integrate with the nervous system responsible for visual processing, it is possible that some ipRGCs axons carry output signals derived from various photopigments [11].

Provencio et al. [5] identified and defined a model of regulation of circadian rhythms through ipRGCs. Initially, this model discusses that light excites a group of photosensitive opsins in ipRGC s cells and later induces the opening of glutamatergic receptors in the suprachiasmatic nucleus. At complex levels, a lasting expression of genes occurs by the joining of some proteins that fit in a period of approximate de 24 h [6, 12, 13].

IpRGCs contain opsins called melanopsins act as light-sensitive photopigments [14, 15]. Melanopsin has signaling time properties in ipRGCs distinct from cones and rods [7, 16, 17], being associated with circadian, neuroendocrine and neurobehavioral functions, besides influencing some imaging functions [18]. Electrophysiological records of ipRGCs have shown lower sensitivity to light in relation to photoreceptor cones and rods [13]. According to the standard view, this photopigment has low sensitivity to light but is able to integrate sustained photic energy.

The peak visual sensitivity of ipRGCs (420 to 480 nm) crosses with the light intensity absorbed by rods and cones (380–650 nm and 440–560 nm, respectively), mainly related to short wavelength and intensity 430 nm (**Figure 1**). Melanopsin adaptation contributes to the relative gain of spectral sensitivity of photoreceptor responses

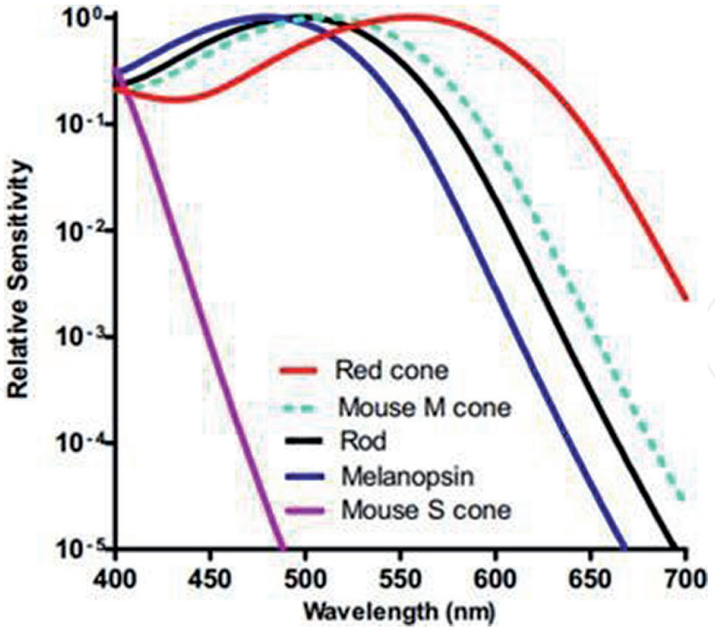

Figure 1.
Discovery of ipRGCs: Approximate spectral sensitivity by opsin nanogram with peak human sensitivity for long-length cones (red line, lmax = 556 nm), peak spectral sensitivity of a rod rat (black line, lmax = 498 nm), melanopsin (blueline, lmax = 480 nm), and cones of short wavelength (purple line, lmax = 360 nm) and medium (dotted line, lmax = 511 nm). Adapted from [19].

to cones and rods in the retina [20]. However, the individual contribution of each class of photoreceptors to irradiance responses is complex [19]. That is, the circadian rhythm system is part of a complex visual system [21].

According to Berson (2003) the photosensitivity of ipRGCs requiring melanopsin conduct various visual functions in the absence of rods and cones. Studies by Tosini [22] and Tosini, Pozdeyev, Sakamoto and Luvone [23] suggest that the retina also has a circadian clock capable of controlling visual processing functions. Numerous studies have shown that visual sensitivity, defined by means of visual contrast thresholds, has a circadian behavior in several species, among them: zebras [24], Larval Xenopus [25], rats [26], and humans [27–30]. These results, in general, culminate the idea that the filtering of properties of human visual processing occurs according to the circadian variation of visual sensitivity. Therefore, ipRGCs cells constitute a third class of photoreceptors, in addition to rod cells and cones, which are responsible for the formation of the image or visual scene during a 24-hour rhythm.

Remember that rods and cones ingrate ipRGCs and, consequently, circadian behaviors may be associated with these mechanisms. Recent findings have shown that mechanisms that process the contrast of luminance and color are associated with the circadian timing pattern [27, 31].

3. Circadian rhythms of sensation and visual perception

Circadian rhythms modulate the physiology and behavior of animals and humans, so it is important to analyze which aspects of visual perception present circadian variations. Next, we describe the evidence that exists about circadian rhythms in the sensation and perception of contrast, as well as the sensation and perception of the contrast of luminance and colors.

3.1 Daily variation of sensation and perception of contrast of luminance

Melanopsin can contribute by balancing spatial and temporal resolution and optimizing visual sensitivity performance, even at low response levels [32]. Studies on the relationship between circadian mechanisms and visual sensitivity of luminance are still considered contradictory. However, electrophysiological and psychophysical studies have raised preliminary hypotheses about the circadian influence on the discrimination of the visual threshold of luminance contrast. Spatial variation in light intensity, called spatial contrast, comprises much of the visual information perceived by mammals, and the relative ability to detect contrast is called contrast sensitivity [33].

As previously seen, Turner and Mainster [34] argue that retinal ganglion cell photopigments contribute to the circadian modulation of visual sensory function [35, 36]. O'Keefe and Baker [37] used the psychophysical method of constant stimulus to measure diurnal variations in visual sensitivity in photon and scotopic luminance conditions. This study showed higher visual sensitivity in photon conditions compared to scotopic sensitivity. In addition, the visual sensitivity of the individuals varied according to the daily time, presenting greater visual sensitivity at night. Using a similar psychophysical method, Tassi et al. [30] suggested that human sensitivity changes during the 24-hour period and that circadian rhythm has an influence on visual sensitivity in both scotopic and mesopic luminance conditions (0.007 and 0.021 cd/m^2).

Tassi et al. [30] used a daily routine chronobiological protocol that provides a schematic representation of the subject's responses during the peaks inactivity. The authors scored eight measurement points with alternation of 2 h during the period from 08:00 to 20:00 hours, and showed changes in visual sensitivity throughout the day, with decreased sensitivity in the morning and progressive increase throughout the day, reaching its peak at 22:00. It was also observed that the sensitivity remained high during the first half of the night and progressively decreased after 04:00 in the morning.

Bassi and Powers [28] argued that temporal visual sensitivity also exhibits variation during the day. The authors measured the visual thresholds of seven subjects between 20 and 38 years old using the psychophysical paradigm of equalization by flashing photometry (flicker) during the periods of (12:00–14:00 and 00:00–02:00). Bassi and Powers noticed a small fluctuation in visual sensitivity and concluded that the ability to detect light varied systematically according to the periods indicated, showing minimal sensitivity during 12:00–14:00 and presenting maximum sensitivity at 00:00–02:00.

Although the findings indicated visual circadian alterations, the studies did not pay attention to verifying whether this variation differed according to the circadian typology of the participants, that is, whether the circadian modulation of visual sensitivity has different characteristics between subjects with behavioral patterns of morning activity and rest, intermediates and afternoons. In 1997 Tassi and Pins used the Horne and Ostberg Questionnaire to characterize the circadian typology of seven subjects and measured binocular visual sensitivity with a psychophysical method of adaptation between 08:00 and 18:00. The authors observed that visual sensitivity was low during the morning shift and increased progressively from 10:00 am, remaining constant until 18:00 hours.

The results for low sensitivity in the morning shift were only for three subjects with intermediate chronotype, while the sensitivity that remained constant was for

the subjects with morning and afternoon chronotype. Still, Tassi and Pins argued that visual reaction time is significantly longer during the night period, and the proportion of responses between the sexes indicates that men have greater stability than women. In general, the authors suggest that this phenomenon of sensitivity variation is not a general rule since subgroups could be isolated in samples considering their circadian typology, in addition several mechanisms can contribute to fluctuation of visual sensitivity, such as the rhythmic expression of melatonin and dopamine in rods and photoreceptors and cones.

3.2 Daily variation in contrast sensitivity

The ability to detect and interpret details of a visual scene is determined by the visual system's ability to distinguish contrast patterns [38]. Contrast can also be understood as the physical property of the visual stimulus, and the magnitude of the variation of luminance in the stimulus related to the total luminance of adjacent areas [38].

In this sense, the visual system (SV) has high sensitivity when a pattern needs little contrast to be detected. The reverse, low sensitivity, when the SV needs high contrast value to detect the stimulus. The contrast sensitivity curve represents the sensitivity of the SV in being more or less sensitive at certain spatial frequencies [33, 39]. The frequency of a sine wave in a visual experiment is described by visual angle degree cycles, which corresponds to the number of grid cycles that subtend 1 degree of angle to the human eye [40]. The Contrast Sensitivity Function (CSV) of numerous thresholds describes an inverted U-shaped curve with low frequency inclination and a steep slope in high frequencies [38]. From a practical point of view, CSV can be measured through psychophysical or behavioral criteria [41]. Physiologically, these channels refer to neuronal populations involved in the selective processing of spatial frequency bands [42]. Thus, it is believed that the process of detecting visual contrast is due to the activity of one or more spatial frequency channels, the variations of these frequencies are broken down into bands tuned to low, medium and high spatial frequencies.

Thus, it is possible to discriminate the minimum amount of contrast that the SV needs to individually detect each range or spatial frequency band since the response of one channel is not affected by the response of the other. So far, the big question discussed is whether there is a circadian rhythm of CSV, that is, that there is a circadian SV of contrast sensitivity of spatial frequencies.

Struck, Rodnitzky, and Dobson [43] used sine wave grid stimuli to measure CSV. Struck et al. [43] evaluated the contrast sensitivity of 12 participants with Parkinson's disease (PD) using low, medium and high spatial frequencies (1, 5, 3, 6, 12 and 18 cpg). The authors found punctual circadian fluctuations with lower dysfunction in the early morning compared to the afternoon. At 8:30 a.m., sensitivity in participants did not differ from healthy subjects, but as hours passed, the results were significantly worse at 3 or more spatial frequencies (3 and 6 cpg). CSV for healthy subjects remained constant over time, unlike the findings on visual circadian fluctuations found by Bassi and Powers [28], O'Keefe and Baker [37], Tassi and Pins [29], and Tassi et al. [30]. For Struck et al. [43], the variation in contrast sensitivity in spatial frequencies was related to dopamine deficiency caused by PD.

Recent studies prepared by Andrade, Silva, and Santos [44] and Andrade et al. [27, 31] evaluated CSV circadian fluctuation in healthy adult subjects according to circadian typology at different times of the day. These studies indicate that CSV

curves have minimum sensitivity at 09:00, progressive increase from 13:00 to 17:00 and maximum sensitivity at 21:00. During the periods of 13:00 and 17:00 the measurements remain constant. Also, morning subjects present peak sensitivity in the morning, but are less sensitive than afternoon subjects throughout the day.

Andrade et al. [44] measured the CSV of 18 male subjects using the daily routine chronobiological protocol and the psychophysical method of the ladder to measure stimuli of vertical sine grid in a condition of photopic (41.9 cd/m^2). The results showed that morning subjects have maximum sensitivity at 7:00 a.m. when compared to the 3:00 and 11:00 times, mainly at the spatial frequency of 3.1 cpg; intermediate and vespertine subjects presented maximum sensitivity at 23:00 for spatial frequencies of 0.6 and 3.1, 6.1 and 8.8 cpg, respectively. It is possible to observe a fluctuation in CSV as seen by Bassi and Powers [28]. Thus, in addition to the variation in daily luminance contrast, the findings also indicated differences in sensitivity according to circadian typology in relation to specific spatial frequencies. This study demonstrated that visual contrast adaptation depends on behavioral and cognitive factors such as sleep latency, drowsiness levels, alertness and visual attention. From this point, Andrade et al. [44] highlight the needs of psychophysical research that evaluates basic visual functions in terms of chronobiological rhythms, such as the measurement of CSV in circadian time [45].

Andrade et al. [27, 31] also evaluated CSV according to circadian typology and measurement time of adult men (M = 23.42 ± 2.6 years) during a daily period. The authors observed that CSV curves had decreased sensitivity for low and high spatial frequencies [46] and peak sensitivity for average spatial frequencies [42]. The results did not show variation in CSV of morning subjects, but detected fluctuation in CSV for night subjects with greater sensitivity in the period of 21:00 in spatial frequencies of 1.0, 3.1 and 13.2 cpg, and fluctuation in CSV for intermediate subjects in spatial frequencies of 0.2 and 15.6 cpg. Furthermore, the study by Andrade et al. [27, 31] pointed out that intermediate subjects have maximum sensitivity in spatial frequency 0.2 cpg at 17:00 when compared to 9:00 and 13:00 times. There was an attenuation in visual sensitivity during the morning in all groups, except for morning subjects. In general, the study by Andrade et al. [27, 31] proposes greater visual sensitivity in the CSV curve during the night period (21:00) and a decrease in sensitivity at 09:00. According to Viola et al. [47] it is common to observe greater variation in behavioral measures of venous subjects due to evolutionary traits and circadian genetic expression of these subjects, i.e., venous subjects have a genetic repeat polymorphism PER3$^{4/4}$ more vulnerable to daily fluctuation, when compared to the genetic expression of morning subjects PER3$^{5/5}$ and intermediate subjects PER3$^{4/5}$. Furthermore, evening subjects have a tendency to sleep delay (2 h) in relation to other subjects, thus night vision adapts melatonin production and masks the significant effect of spatial resolution of photoreceptors rods and cones [48].

Both results described by Andrade et al. [44] indicate maximum sensitivity at 07:00/09:00 compared to 15:00 and 23:00 for morning subjects and maximum sensitivity in the periods of 15:00 and 23:00 for intermediate and vespertine subjects, characterizing possible patterns of behavior of CSV according to circadian typology.

Daily changes in visual sensitivity can explain many factors about the effects of light on visual contrast perception. In fact, the visual system is not linear and the visual sensitivity curve presents daily variations according to visual space and time [44], however these variations may be related to circadian behavior of CSV (**Figure 2**). Thus, the relationship between homeostatic and circadian variables establishes a daily control of the detection of visual thresholds of luminance contrast [27, 31].

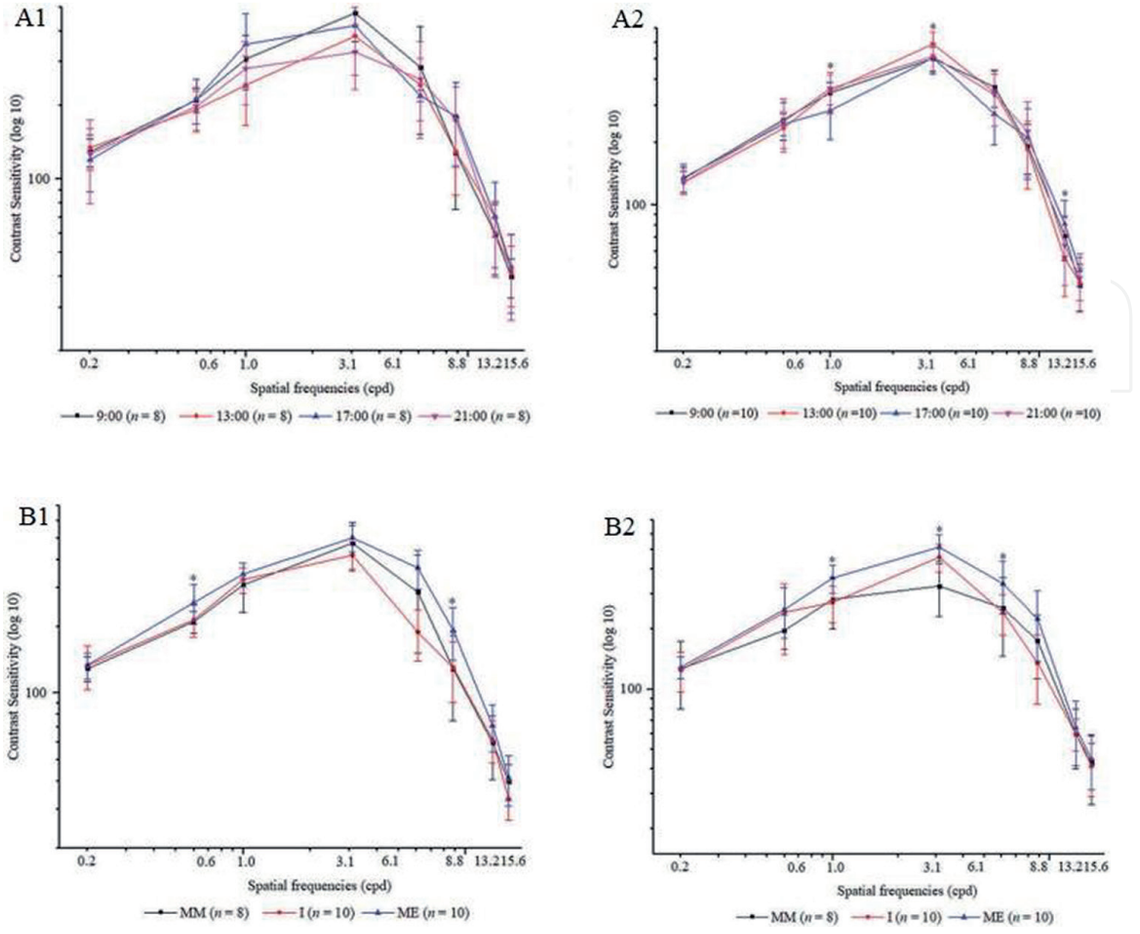

Figure 2.
Circadian behavior of the visual contrast curves: (A) contrast sensitivity curves obtained during the 24-hour period according to the time: (A1) represents the variation of the contrast in spatial frequencies for the moderately morning participants (MM); represents the variation of the contrast in the spatial frequencies for the participants of the moderately afternoon (MV); (B) contrast sensitivity curves obtained during the 24-hour period for participants MM, MV and intermediates (I): (B1) represents the variation of contrast in spatial frequencies at 9 am; (B2) represents the variation of contrast in spatial frequencies at 9 pm. Taken from Andrade et al., [27, 31].

3.3 Daily variation of sensation and perception of colors

In recent decades, the study of color perception has stood out due to its functional role in the visual perception process of subjects with normal vision and deviations in the axes of color confusion. In general, the human view of color is considered trichromatic and its modification results from congenital defects or is acquired by adverse situations [49]. A set of photoreceptor cells in several visual sensitivity levels can absorb and combine wavelengths to form three-dimensional color perception at any point in the visual field [50, 51].

The variability of light absorption in the retina by cones shows that opsins are sensitive to wavelengths in the range of 400 to 700 nm; their absorption intensity varies according to the selectivity of the three classes or wavelength peaks, that is, to red (559 nm), green (531 nm) and blue (419 nm). It is appropriate to refer to the three types of cone as long, medium and short wave, respectively. According to Figueiro, Bullough, Parsons and Rea [52], the physiological aspects of retinal imaging are still subject to a biological change in time caused by circadian rhythm. Psychophysical studies show that color perception can be evaluated based on the capacity of equality and discrimination of thresholds [51, 53]. Studies have investigated the circadian mechanisms of color perception [54, 55].

Pauers et al. [55] suggest that the color opposition mechanism is evolutionarily adapted to the spectral changes of sunlight during the earth's rotation. In addition, the spectral positioning of the short wavelength S (absorption for blue color perception) may be directly related to the determination of these patterns of activity.

According to a study conducted by Danilenko et al. [56], a greater capacity of activity of cones during the night and a decrease in response in the early morning was reported through an electroretinogram during a constant follow-up of 24 hours of white light. The data indicate that there is a change in the perception of color during a circadian rhythm, but it is not clear in relation to the period, amplitude and phase in which it occurs. For Ebihara and Tsuji [57] and Mrosovsky [58], melanopsin also contributes to the synchronization of circadian rhythm activity of visual color. However, it is possible that a number of behavioral and physical variables, such as the light/dark cycle, exposure to light and circadian typology determine variations in the axes of color confusion [59]. Thus, studies start from hypotheses that there is a daily modulation of visual color perception in the long, medium and short wavelength confusion axes [31].

Andrade et al. [27, 31] measured the circadian rhythm of the color confusion axes of 28 young male adults aged between 20 and 28 years according to their circadian typology using the Cambridge Color Test (CCT) and the Lanthony Desaturated D-15d test). This study suggested that the neural processing of color perception in the green-red axis has a daily fluctuation, especially for night subjects. In addition, the vespertine subjects presented higher visual sensitivity in the protan, deutan and tritan axes, especially in the periods of 9:00 and 21:00 and morning subjects had lower visual sensitivity at 13:00 and 17:00. To Archer et al. [60], morning subjects are more stable in relation to fluctuations in behavioral responses. It is normal that there is a variation of the visual thresholds during the day, and that they present normal parameters for trichromatic subjects [61], however it is possible that this variation has characteristics according to circadian typology and measurement times.

The modulation in the operation of the green-red and blue-yellow confounding axes may be related to the interactions of wavelength absorption by ipRGC cells (420 to 480 nm) that intersect with the light intensity absorbed by the rods and cones (380-650 nm and 440–560 nm, respectively). Thus, Tritan axis stability is intrinsically related to the constant absorption of melanopsin and stability of the daily fluctuation of the blue wavelength [22, 62, 63]. Danilenko et al. [56] suggest that the spectral position of the medium and long wavelength suffers less influence of melanopsin pigment activity, allowing the daily fluctuation of chromatic sensitivity. According to Walmsley et al. [64] the variation of these spectral changes is necessary for circadian alignment of information, keeping natural conditions constant. It is a note point that the daily entrainment of sleep capacity can contribute significantly to the daily adaptation of visual perception [27, 31].

Thus, it is possible to characterize chromatic rhythmic changes of the visual system according to exposure to light, however the results for color perception are considered preliminary [65].

4. Final considerations

In the present work, we reviewed the theoretical and experimental knowledge discovered about the interaction between the visual system and the circadian system. A visual path was found that participates in the synchronization of circadian

rhythms. Light produces synchronization of circadian rhythms by activating intrinsically photosensitive retinal ganglion cells (ipRGCs). These cells use melanopsin as a photopigment and modulate the activity of the suprachiasmatic nucleus of the hypothalamus, which acts as a central pacemaker of circadian rhythms. The analysis of the functioning of the visual path that synchronizes circadian rhythms is important to understand how the human being adapts to schedule changes, such as transnational air travel, night work, or rotating shifts. This visual path is also relevant to understanding changes in response to light, which have been observed in patients with circadian rhythm disorders, such as: circadian rhythm sleep disorder, seasonal depression or manic-depressive disorder. In addition, knowledge of this visual pathway is important to analyze the physiological effects of light (phototherapy), when used as a treatment for circadian rhythm disorders, as well as other neurological and psychiatric disorders.

On the other hand, circadian rhythms were found in submodality of visual sensation and perception, such as contrast of luminosity, color discrimination and perception of objects, and images. These rhythms in visual perception are modulated by people's chronotypes. The study of circadian rhythms in visual perception can be important for the learning of visual and visuospatial tasks, as well as for performance in school or work activities that require more specific visual processes, such as contrast of magnifying detail or color perception. In the meantime, it is also important to analyze the interaction of circadian rhythms in visual perception with rhythms of other cognitive processes, such as attention, memory and executive functions; as well as the role of these rhythms in work performance.

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