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# MODELLING NON-VISUAL RESPONSES TO LIGHT: UNIFYING SPECTRAL AND TEMPORAL CHARACTERISTICS IN A SINGLE MODEL STRUCTURE

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## Abstract

The discovery of a novel type of photoreceptor that mediates non-visual light responses in humans has sparked a growing interest in the role of lighting design on human health and wellbeing. Researchers have identified intensity, spectrum, duration/pattern, history, and timing of light exposure as important variables that control the responsiveness of the non-visual system. All of these variables need to be considered when developing a model of non-visual light responses. Currently, there is no mathematical model that incorporates all five variables to predict the non-visual effects of light on humans. In this paper, a modular model structure is proposed towards this end. The model is represented by a sequence of different blocks or elements. Based on a part of this model, which takes into account the intensity, spectrum, and duration of light exposure, it is possible to compare the spectra of different light sources in terms of non-visual driven efficiency. This model provides a framework that can inform designers about how lighting improves human health.

*Keywords*: Light, Photoreceptors, Spectral Efficiency, Circadian, Non-visual, Design

## 1 Introduction

Visible light is not only necessary for seeing but also for resetting and shifting the circadian clock. Each day the circadian clock regulates important physiological and behavioural rhythms, such as sleep-wake cycles, alertness and performance patterns, core body temperature (CBT), and hormone production. In addition to visual and circadian effects of light, exposure to bright light at night can directly suppress melatonin and reduce sleepiness compared with dim light (Cajochen et al., 2000; Zeitzer et al., 2000). Moreover, there is evidence that daytime bright light exposure (above 1 000 lx) reduces sleepiness and improves performance (Phipps-Nelson et al., 2003; Rüger et al., 2006).

These biological or non-visual effects of light are mediated primarily via a novel, non-rod, non-cone photoreceptor that contains the photopigment melanopsin. Melanopsin is more sensitive to short-wavelength light with a peak sensitivity that is blue-shifted ($\lambda_{max} \cong 480$ nm) relative to the photopic visual system ($\lambda_{max} = 555$ nm), which is dominated by the response of cone photoreceptors. In addition to the spectral differences between the sensitivities of the photoreceptors, the non-visual system exhibits different sensitivity to variations in the intensity, duration/pattern, history, and timing of light exposure as compared to vision. Based on the blue-shifted sensitivity of the melanopsin-containing photoreceptors, long-duration short-wavelength light exposure has been shown to be more effective at enhancing alertness and performance (Lockley et al., 2006). Although the melanopsin-containing photoreceptors are the primary photoreceptors for non-visual responses, there may be multiple mechanisms by which light can stimulate different types of photoreceptors to enhance different types of non-visual responses. A recent study hypothesizes that short intermittent dim light pulses having wavelengths in a narrow band around 555 nm can maintain a sustained non-visual response by stimulating cone photoreceptors (Gooley et al., 2012). However, the relative contribution of rods, cones, and melanopsin-containing photoreceptors to the non-visual responses in humans is unclear (Lall et al., 2010).

The current recommendations for lighting in different work and residential spaces are based mainly on visual criteria measured in photometric quantities, such as illuminance. Although

these illuminance levels are sufficient to support visual tasks, such levels do not necessarily ensure enough light to synchronize circadian rhythms to the 24-hour day or promote other physiological and behavioural non-visual responses. The discovery of the melanopsin-containing photoreceptors has led to the consideration that non-visual effects of light are as an important part of good lighting design as visual effects. There are many potential lighting applications to be considered using the information about these novel photoreceptors. The fields of potential applications range from light therapy for the treatment of seasonal depression to lighting design and engineering in buildings. The challenge is to predict the suitability of light exposure in terms of non-visual responses to light throughout the day and night. Currently, there exists no accepted methodology to evaluate different lighting conditions based on the spectral and temporal characteristics of the light source. In this paper, a modular block-structured model is proposed to predict the response of the non-visual system to the intensity, spectrum, duration/pattern, history, and timing of light. The structure consists entirely of elements with a clear physiological interpretation and aims to bring together experimental and theoretical perspectives. As a part of this model, the relative contribution of melanopsin-containing and cone photoreceptors is simulated to compare the non-visual driven efficiency of different light sources.

## 2 Spectral and temporal characteristics

### 2.1 Spectral sensitivity

It is well known that the human retina has two types of visual photoreceptors, cones and rods, with very different spectral characteristics that can be described with spectral efficiency functions. The photopic efficiency function $V(\lambda)$ peaks around $\lambda_{max}$ = 555 nm and corresponds to the spectral sensitivity of cones, which operate when light is plentiful (1 cd·m$^{-2}$ to $10^6$ cd·m$^{-2}$). The scotopic efficiency function $V'(\lambda)$ has a peak sensitivity around $\lambda_{max}$ = 505 nm and describes the spectral sensitivity of rods, which operate when light is very limited ($10^{-6}$ cd·m$^{-2}$ to $10^{-2}$ cd·m$^{-2}$). There is a large gap in the luminance range between photopic and scotopic vision, namely between approximately $10^{-2}$ cd·m$^{-2}$ to 1 cd·m$^{-2}$. In this range, which is called the mesopic condition, both rods and cones provide an input to the visual system. The photopic and scotopic functions have been standardized by the Commission Internationale de l'Éclairage (CIE) and are shown in Figure 1 (a).

A spectral efficiency function of circadian responses, called the circadian efficiency function, has been proposed by Rea et al. (2002) and Gall and Bieske (2004) based on the effects of light on nocturnal melatonin suppression, which responds maximally to light between 446 nm and 483 nm (Brainard et al., 2001; Thapan et al., 2001). The circadian efficiency function proposed by Gall and Bieske (2004), shown in Figure 1 (a), has a peak sensitivity around $\lambda_{max}$ = 460 nm. As a complement to the circadian efficiency function, Enezi et al. (2011) has proposed a melanopic spectral efficiency function that has been derived from a 480 nm opsin nomogram based on the spectral efficiency of melanopsin. The melanopic spectral efficiency function, shown in Figure 1 (a), includes corrections for lens absorbance and optical power, which causes a shift in the peak sensitivity from $\lambda_{max}$ = 480 nm to $\lambda_{max}$ = 488 nm. However, a spectral efficiency function for the human non-visual system has not been standardized because the non-visual responses to light, including melatonin suppression, phase shifting, and alertness, cannot be predicted by a single spectral efficiency function (Güler et al., 2007; Rea et al., 2011; Revell et al., 2010).

The melanopsin-containing photoreceptors are the primary photoreceptors for non-visual responses to light, although these photoreceptors receive an input from the rod and cone photoreceptors (Güler et al., 2007). Recent findings suggest that cone photoreceptors contribute identically to non-visual responses at the beginning of a light exposure and at low irradiance, but that melanopsin dominates the response to long duration light exposures and at high irradiances (Gooley et al., 2010). During exposure to continuous light, melanopsin-containing photoreceptors drive sustained responses to light, but the relative contribution of cone photoreceptors to non-visual responses decreases over time (Gooley et al., 2012). Because of the difference in temporal properties between cone and melanopsin-containing photoreceptors, the magnitude of non-visual responses will depend on both the spectral distribution and temporal characteristics of the light stimuli. Different light sources have very different spectral power distributions (SPD), as illustrated in Figure 1 (b, c). Thus, light

exposures of different durations may produce sensitivity functions with different weights for the relative contribution of cone and melanopsin-containing photoreceptors.

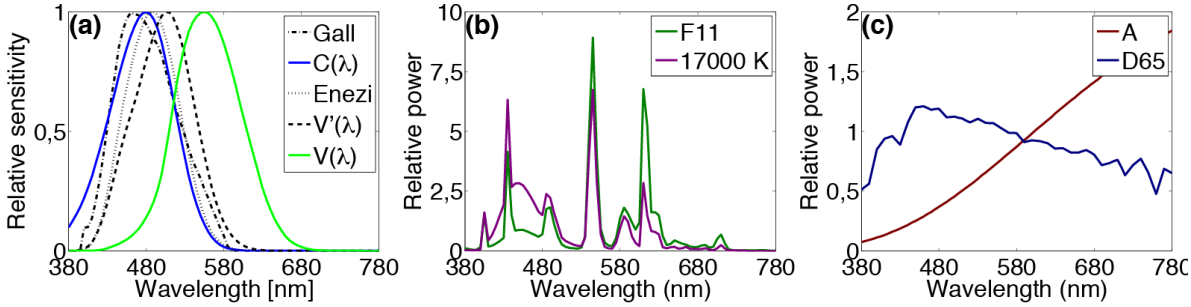


**Figure 1 – (a) The relative spectral sensitivity of the circadian function (Gall and Bieske, 2004), Lamb's photopigment nomogram for melanopsin C(λ) (Lamb, 1995), the melanopic function (Enezi et al., 2011), the scotopic V′(λ) and photopic V(λ) functions. The spectral power distributions of (b) F11 and 17 000 K fluorescent lamps and (c) A and D65 standard illuminants. The light sources are matched for irradiance.**

## 2.2 Light intensity and duration

Brighter light exposures appear to be more effective than dim light in terms of melanopsin-driven non-visual responses. A nonlinear intensity-response relationship between nighttime light exposure and various non-visual responses, including melatonin phase shifting, melatonin suppression, and subjective alertness has been shown (Zeitzer et al., 2000; Cajochen et al., 2000). Moreover, light exposure does not need to be continuous to have an effect on the non-visual system. Several studies have shown that brief intermittent exposures to bright light have a significant effect on phase shifts of the circadian clock (Gronfier et al., 2004; Rimmer et al., 2000). More recently, a study of the pupillary constriction response has shown that melanopsin-containing photoreceptors do not respond to individual intermittent light exposures of low irradiance, but instead appear to integrate the light over time until reaching a steady response (Gooley et al., 2012).

The results of several recent studies indicate a nonlinear relationship between light duration and the magnitude of non-visual responses to light. A single brief exposure to bright light has also been shown to be highly effective for shifting the phase of the circadian clock, suppressing melatonin, and enhancing alertness (Chang et al., 2012). A single 12-minute exposure of bright light (~10 000 lx) induced a 1-hour phase shift as compared with a similarly timed 240-minute exposure that induced a 2,7-hour phase shift. Furthermore, another recent study has demonstrated that a 1-hour bright light pulse shifted the circadian clock by ~2 hours compared with results from a previous study in which a 6,7-hour bright light exposure shifted the clock by ~3 hours (Khalsa et al., 2003; St. Hilaire et al., 2012).

## 2.3 Prior light history

In addition to the nonlinear intensity and duration responses to light, previous light history has also been shown to affect the threshold of non-visual responses (Chang et al., 2011). The study by Chang et al. (2011) has shown that exposure to 1 lx during each wake episode for 3 days resulted in an ~68% increase in the melatonin suppression response compared with exposure to 90 lx for 3 days.

## 2.4 Timing of light exposure

The human circadian system is responsive to light throughout the waking day. The response of the circadian system to the timing of light exposure is described by a phase response curve (PRC) (Khalsa et al., 2003; St. Hilaire et al., 2012). Exposure to light in the biological night prior to the minimum of CBT results in phase shifts to later clock hours (phase delays), whereas exposure to light following the minimum of CBT results in phase shifts to earlier clock hours (phase advances). Most laboratory studies have investigated the non-visual effects of light at night when maximum melatonin suppression and circadian phase shifts occur. However, studies have shown that both nighttime and daytime bright light increases subjective alertness and performance (Phipps-Nelson, et al. 2003; Rüger et al., 2006).

## 3 Model structure

The aim of this study is to develop a model that can predict the non-visual efficiency of different light exposure patterns and inform designers about how lighting improves human health. The behaviour of the non-visual system is dynamic. Therefore, a large amount of data is needed to identify the light-response relationships and interactions between the five characteristics of light exposure: intensity, spectrum, duration/pattern, history, and timing. In the previous section, behaviour patterns are identified through published data. How to incorporate them into a single model structure is discussed in this section.

### 3.1 Single photoreceptor

The model structure comprises three blocks: two blocks that contain linear filters separated by a block that contains a static nonlinear intensity-response function. Figure 2 (a) shows the structure of the human light-response (HLR) model. This type of model structure is referred to as a linear-nonlinear-linear (LNL) model. The model's equations are

$$r(t) = N(l(t) * L_1(t)) * L_2(t), \quad (1)$$

where the asterisk $*$ represents the infix convolution operator. We can rewrite the equation for the output of each block as:

| | |
|---|---|
| $u(t) = l(t) * L_1(t)$ | The light stimulus $l(t)$ is passed through a linear filter $L_1(t)$, which is associated with the temporal integration of the retina, to determine the output $u(t)$; |
| $v(t) = N(u(t))$ | The output $u(t)$ is transformed by a static nonlinear function $N(u(t))$, which describes the intensity-response relationship to the light stimulus, to determine the output $v(t)$; |
| $r(t) = v(t) * L_2(t)$ | The output of $N(u(t))$, $v(t)$, is passed through a second filter $L_2(t)$, which reflects the adaptation of the non-visual system to continuous light exposure, to determine the final output $r(t)$. |

The two filters, $L_1(t)$ and $L_2(t)$, reflect the temporal processing between the light stimulus and the output response. The area of the filters, $L_1(t)$ and $L_2(t)$, is equal to unity, which means that the filters neither amplify nor reduce the total response. The outputs of the filters depend on both the current and past inputs and therefore simulate the adaptation of the non-visual system to current and past light exposures.

The relative response is determined by the choice of the static nonlinear term. The intensity-response functions for phase shifting, melatonin suppression, and alerting effects are all best fit by a 4-parameter logistic function with a half maximum response around 100 lx (4 100 K polychromatic fluorescent light source) (Zeitzer et al., 2000; Cajochen et al., 2000). The equation for the 4-parameter logistic function is used to represent the static nonlinear term

$$N(u) = \frac{a-c}{1+(u/b)^d} + c, \quad (2)$$

where $a$ is the estimated response of the system to no light, $b$ is the intensity value at which 50% of the maximal response is observed, $c$ is the maximal responsiveness of the system, and $d$ is the slope of the function.

The $L_2(t)$ linear filter was derived by taking the inverse of the duration-response curve to phase shifts that was published by Chang et al. (2012) with length set to 6,5 hours. The output response and the $L_2(t)$ filter are time-reversed copies of each other, as demonstrated in Figure 2 (a). This duration-response curve demonstrates that the highest rate of activation of the system occurs at the onset of the light exposure and saturates after a few hours of continuous light exposure (Chang et al., 2012), Figure 2 (b).

The length of the $L_1(t)$ linear filter can be estimated from experimental data. An average filter with a length of 39 minutes can replicate the results in Gronfier et al. (2004), in which a single sequence of intermittent bright light exposure (23% of the total exposure time) was 77% as effective as a continuous bright light exposure (100% of the total exposure time) at phase delaying the circadian system. If $L_1(t)$ is set to unity, then the model structure corresponds to

the nonlinear-linear (NL) model, which consists of a static nonlinearity followed by a linear dynamic subsystem. The NL model underestimates the performance of intermittent light patterns compared with experimental observations and predicts only 30% of the maximal response effect. Using an average filter with a length of 39 minutes, the LNL model overcomes this problem and accurately simulates the observed behaviour (Figure 2 (b)).

The proposed model has the potential to capture the non-visual effects of time-varying light exposure. Here we have demonstrated the selection of model parameters for light exposure at 10 000 lx based on the available phase shift data. Since the interactions between intensity and duration are currently unknown, we assume that the duration-response relationship is the same at different light intensities, spectra, and times of day. Further, the model is not limited to the melatonin phase-shifting response and can be adapted to any non-visual response, which allows for more flexibility as knowledge accumulates.

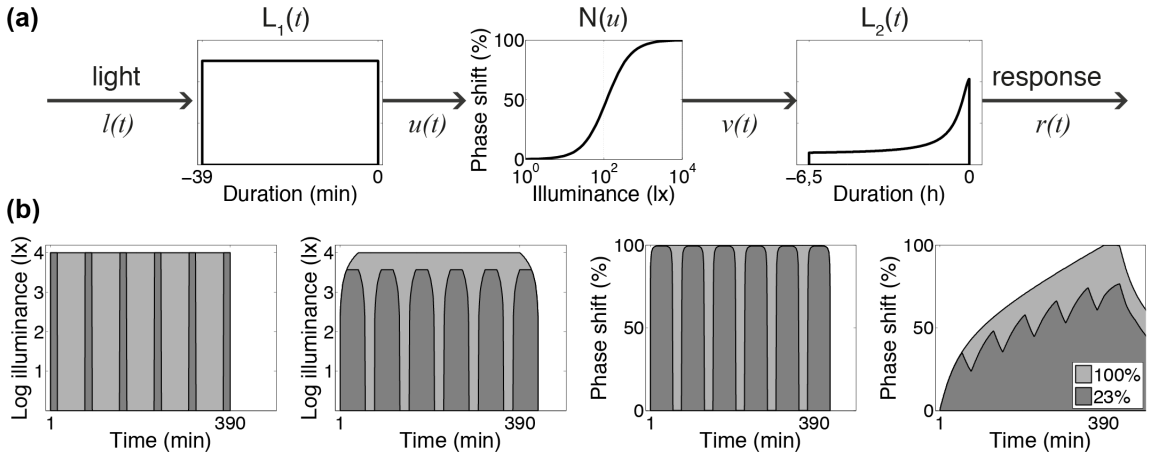


**Figure 2 – Demonstration of the HLR model based on the available phase shift data for melatonin suppression. (a) A diagram of the LNL model structure. (b) The process of transforming light input into response output for two light patterns.**

## 3.2 Dynamic regulation of photoreceptors' responses

The effect of prior light history may be due to the adaptation of the response of the melanopsin-containing photoreceptors to light and affects the intensity threshold of the non-visual response. Increasing or decreasing the half-saturation intensity value depending on previous light exposure history can explain the dynamic response of the non-visual system. A feedback loop was added as a fourth block in the model to extend the dynamic range of the system and to produce a dynamic intensity-response curve, Figure 3 (a). By shifting the half-saturation intensity value in the positive direction of the x-axis (Figure 3 (b)) the dynamic range increases and the system is capable of responding to a broader range of light intensities. By shifting the half-saturation point back along the negative direction of the x-axis, the dynamic range decreases (Figure 3 (c)). Such a simple mechanism can account for current experimental observations. As an example, the study by Chang et al. (2011) demonstrated that a dim light history sensitizes the non-visual response compared with a typical indoor light history.

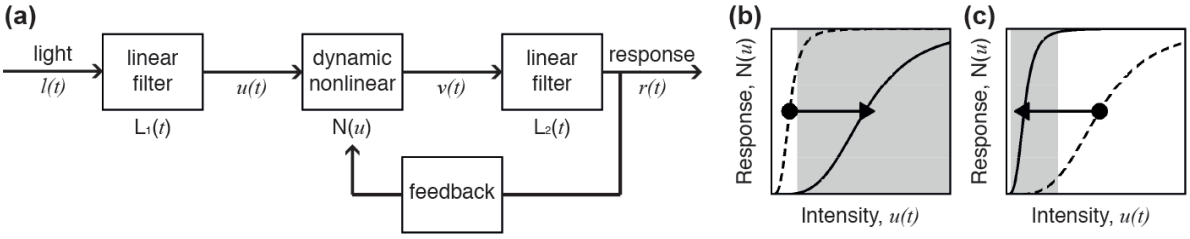


**Figure 3 – (a) A diagram of the HLR model including feedback loop to account for time-varying responses. (b) Feedback can extend the dynamic range (grey area) of the response or (c) reduce it so that the sensitivity at low light intensity is increased.**

### 3.3 Interaction of two photoreceptors

The spectrum of the light stimulus that is given as an input to the HLR model must be weighted according to the spectral sensitivity of the non-visual system. A transition from a predominantly cone-based response to a predominantly melanopsin-based response causes a shift in the peak wavelength sensitivity from 555 nm to 480 nm. If we assume that the sensitivity of the two photoreceptors is additive, the sensitivity of the non-visual system can be expressed as a weighted linear combination of the luminous efficiency function, $V(\lambda)$, and the melanopsin-driven efficiency function, $C(\lambda)$

$$w(t)\,C(\lambda) + \big(1 - w(t)\big)\,V(\lambda), \tag{3}$$

where the weights change with time $t$, $w(t)$ is the relative contribution of the melanopsin-containing photoreceptors, and $1-w(t)$ is the relative contribution of the cones at time $t$. In order to compute the weights in Equation (3), we propose to use Lamb's photopigment nomogram (Lamb, 1995) to construct a spectral sensitivity function for melanopsin-containing photoreceptors with a peak sensitivity at $\lambda_{max}$ = 480 nm, as shown in Figure 1 (a).

A recent study has shown that the sensitivity of melatonin suppression to a 555 nm light exposure decayed exponentially relative to a 460 nm light exposure as the duration of light increased (Gooley et al., 2010). This decay in relative sensitivity was modelled with a 3-parameter exponential decay function. In order to reduce the complexity, a 1-parameter exponential decay function $e^{-t/2}$-1 with a half-life of 1 h 23 min is used to approximate the log relative sensitivity of melatonin suppression. At time $t$ = 0, the log relative sensitivity is 0; after a light exposure duration of 4 h ($t$ = 4), the log relative sensitivity is -0,86. The relative contribution of melanopsin-containing and cone photoreceptors is calculated by solving for $w(t)$ in the following equation

$$e^{-t/2} - 1 = \log_{10}\left(\frac{w(t)\,C(555)+\big(1-w(t)\big)\,V(555)}{w(t)\,C(460)+(1-w(t)V(460)}\right), \tag{4}$$

for all $t$ between 0 and 4. The relative contribution of the two photoreceptors is shown in Figure 4 (a). The difference in relative spectral sensitivity of the non-visual system as a function of time is shown in Figure 4 (b). The black line corresponds to the combined contribution of cones and melanopsin-containing photoreceptors.

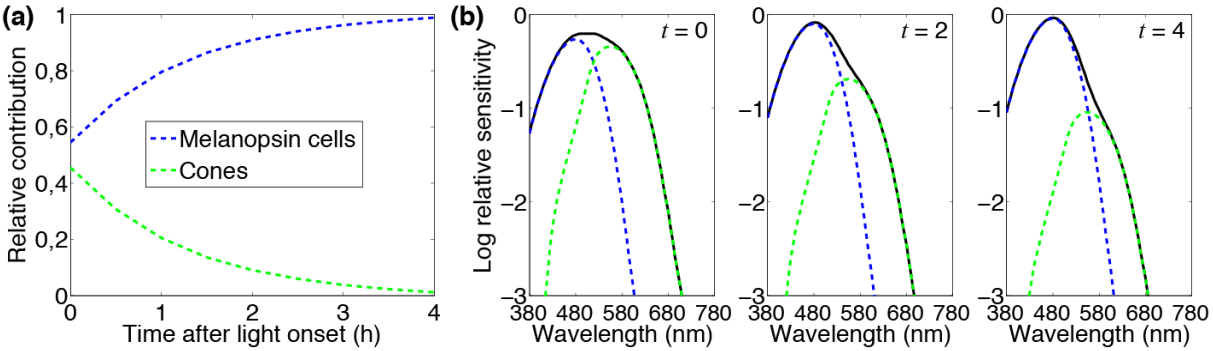


**Figure 4 – (a) At the beginning of a light exposure, the contribution of cones and melanopsin is approximately equal. After 4 hours of continuous light exposure, the contribution is mainly from melanopsin (99%). (b) The transition from a predominantly cone response to a predominantly melanopsin response over time.**

## 4 Comparison of different light sources

The relative efficiency of different light sources to stimulate the non-visual system can be evaluated by simulating the relative contribution of melanopsin-containing and cone photoreceptors using the model in Section 3.3. For a quantitative comparison, it is possible to describe the non-visual effects of different types of light sources using the relative ratio of melanopsin-stimulating illuminance to photopic illuminance. This concept was first introduced by Rea et al. (2002), and was defined as the circadian action factor, $a_{cv}$, by Gall and Bieske

(2004). The light sources with the highest action factor values are those that are more efficient in terms of non-visual responses compared with visual responses. The concept of the $a_{cv}$ has been used to study the melanopsin-driven efficiency of different light sources (Bellia et al., 2011) and to evaluate architectural spaces (Pechacek et al., 2008).

The ratio of melanopsin-stimulating illuminance, $E_c$ (c-lx), to photopic illuminance, $E_v$ (lx), is, as a result,

$$\frac{Ec}{Ev} = \frac{6126 \sum E_{e,\lambda}\, C(\lambda)\, \Delta\lambda}{K_m \sum E_{e,\lambda}\, V(\lambda)\, \Delta\lambda} = \frac{6126}{K_m} a_{cv}, \quad (5)$$

where $E_{e,\lambda}$ is the average value of the irradiance (W·m$^{-2)}$ per wavelength interval $\Delta\lambda$, $C(\lambda)$ is the relative melanopsin-driven efficiency, $K_m$ is a constant equal to 683 lm·W$^{-1}$, $V(\lambda)$ is the relative luminous efficiency, and $a_{cv}$ is the action factor. The melanopsin-stimulating and photopic illuminances are matched at $\lambda$ = 555 nm; therefore, the constant must be $K_m$/C(555) = 683/0,1115 = 6126 c-lm·W$^{-1}$.

To compare light sources, we use the four polychromatic light sources shown in Figure 1 (b, c) and two monochromatic light sources at wavelengths of 555 nm and 480 nm. We include three standard CIE illuminants: a 2 856 K incandescent (A), a 6 500 K noon daylight (D65), and a 4 000 K cool white fluorescent (F11) (CIE, 2006); and a high 17 000 K blue-enriched white fluorescent lamp (ActiViva Active, Philips). Figure 1 (b, c) shows the spectral power distribution of the four illuminants matched for irradiance. The comparison is summarized in Table 1. The light sources are presented in ascending order relative to the $E_c/E_v$ ratio and the action factor $a_{cv}$ (Table 1 (a)). The light sources and two monochromatic light sources are matched so that they deliver the same irradiance in Table 1 (b) and the same melanopsin-stimulating illuminances in Table 1 (c).

**Table 1 – Comparison of irradiance $E_e$, photopic illuminance $E_v$, melanopsin-stimulating-illuminance $E_c$, $E_c/E_v$ ratio, and the action factor $a_{cv}$.**

| | **(a)** Relative ratio | | **(b)** Irradiance, $E_e$ = 0,1 W·m$^{-2}$ | | **(c)** Melanopsin-stimulating illuminance, $E_c$ = 612 c-lx | |
|---|---|---|---|---|---|---|
| **Light** | $E_c/E_v$ | $a_{cv}$ | $E_v$ **(lx)** | $E_c$ **(c-lx)** | $E_e$ **(W·m$^{-2}$)** | $E_v$ **(lx)** |
| 555 nm | 1 | 0,11 | 68 | 68 | 0,90 | 612 |
| A | 4 | 0,44 | 15 | 61 | 1,00 | 154 |
| F11 | 5 | 0,55 | 34 | 167 | 0,37 | 123 |
| D65 | 9 | 1,02 | 20 | 186 | 0,33 | 67 |
| 17 000 K | 12 | 1,38 | 24 | 302 | 0,20 | 49 |
| 480 nm | 64 | 7,19 | 9 | 612 | 0,10 | 9 |

Recent study by Revell et al. (2010) exposed subjects to different types of light sources matched for melanopsin-stimulating illuminance. The results of this study showed that 30-minute exposures to 535 nm, 4 000 K (F11), 17 000 K, and 440 nm light sources were more effective in stimulating alerting effects compared with a 480 nm light source. Figure 5 (a) shows that monochromatic light sources of wavelength 480 nm and 440 nm are less effective at the beginning of a light exposure compared with other light sources when matched for melanopsin-stimulating illuminance. Although, the 535 nm light source has a small overlap with $C(\lambda)$, the irradiance weighted with the duration-dependent curves in Figure 4 (b) is the highest for the 535 nm light source due to the contribution of cones. However, the model cannot explain why the 440 nm light source was found to be more efficient than the 480 nm light source. A possible explanation is that the 440 nm monochromatic light may be able to stimulate short-wavelength cones, which are most sensitive to light at wavelengths around

420 nm, in particular because $V(\lambda)$ is a smoothed and symmetrised representation of the three different cones photoreceptors.

In addition to 4 000 K (F11) and 17 000 K light sources used in the study by Revell et al. (2010), we simulated standard illuminants A and D65. As Figure 5 (a) shows, the melanopsin-driven efficacy of light appears to relate to the relative ratio of the light source but not to the irradiance at the beginning of a light exposure. In the study by Revell et al. (2010), the alerting efficacy of light appeared to relate to the total irradiance of the light source. Figure 5 (b) shows the relative non-visual driven efficiency as a function of time for the light sources listed in Table 1 corresponding to the normalized SPD. The efficiency of 17 000 K increases with time, but decreases for illuminants A and F11. The efficiency of D65 is close to constant, because daylight stimulates both systems at the same time. The light sources that are the least efficient for stimulating non-visual responses in terms of spectral power are rated with lower values.

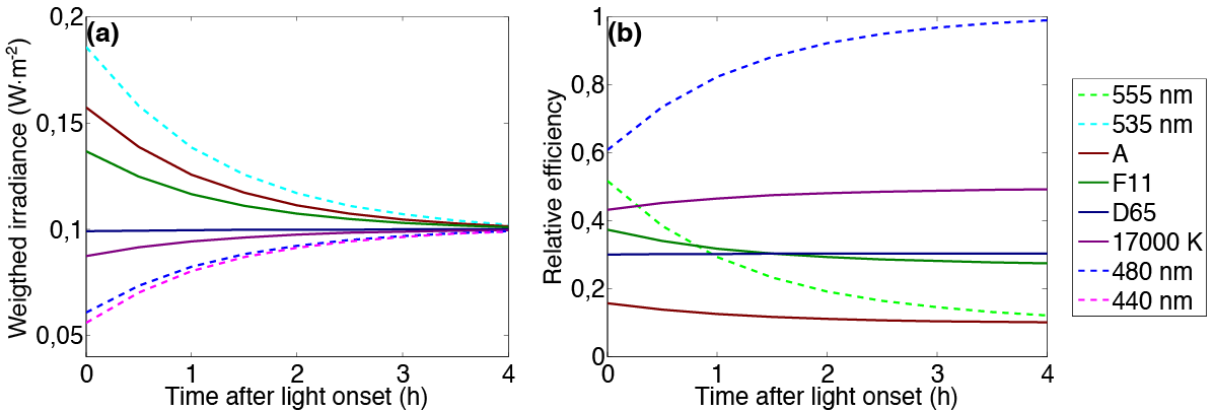


**Figure 5 – (a) Weighted irradiance as a function of time where light sources are matched for melanopsin-stimulating illuminance. (b) Relative non-visual driven efficiency as a function of time where light sources are normalized with the SPD.**

## 5 Discussion

The non-visual responses to light are dependent on light intensity, spectrum, duration/pattern, timing, and history; however, the optimal composition of light remains unclear. Currently, there are no models that incorporate all five light characteristics. In the past, illuminance has been the most important variable in lighting design. However, the spectral sensitivity of the melanopsin-containing photoreceptors is significantly different from rods and cones, which highlights how unsuitable the use of illuminance is to evaluate the non-visual effects of light without any assumptions regarding the underlying SPD of the light source. Therefore, including the light spectrum as a variable in the model allows for lighting design that better addresses the effects of non-visual responses to light on human health.

In real-world situations, exposure to bright light is typically intermittent. Compared with melanopsin-containing photoreceptors, visual photoreceptors can readily adjust their response to changes in light levels. Melanopsin-containing photoreceptors cannot track intermittent light patterns and seem to integrate over time until reaching a steady response at both low and high light intensity levels. Moreover, the highest rate of activation is found at the onset of light exposure, where non-visual responses seem to be sluggish and slower to activate compared to visual responses (Chang et al., 2012). These effects are included in the model by linear filters using duration (the length of the filter) as a variable.

The sensitivity of the non-visual system depends on the timing and history of light exposure. The previous light history affects the intensity threshold of the non-visual responses and the effective light history can extend several days into the past. Therefore, a fourth block in the model is a feedback loop that can extend the dynamic range of the system and produce a dynamic intensity-response curve. Moreover, the effect of light exposure on the non-visual system depends on the timing with respect to the underlying circadian rhythm. A fifth block

can be added to the model that controls the magnitude of response based on the timing of light exposure, which can be described by a phase response curve (Khalsa et al., 2003).

Complexities arise because melanopsin-containing photoreceptors receive input from both rod and cone photoreceptors. Studies have shown that for low light intensities, which are below the threshold of activation for melanopsin, cone and melanopsin-containing photoreceptors contribute identically to non-visual responses (Gooley et al., 2010; Gooley et al., 2012). However, the relative contribution of cones seems to decrease over time during exposure to continuous light. Therefore, the non-visual system should be represented with a time-varying spectral sensitivity function, which is equivalent to a Purkinje shift in which there is a switch from rods to cones with increasing light intensity. The challenge is to characterize how spectral sensitivity changes as a function of light intensity and light exposure duration. In this study, we modelled the non-visual sensitivity curves as a weighted linear combination of the melanopsin-driven and the luminous efficiency functions. These simplified assumptions explain experimental findings on the non-visual effect of light at the beginning of light exposure and under low light conditions (Revell et al., 2010).

The photoreceptors signal to the brain through different pathways and can stimulate different parts of the brain, which may explain why the mechanisms of all non-visual responses are not identical. Phase-shifting effects and melatonin suppression responses are slow to activate, but direct effects such as alerting effects and pupillary constriction seem to be immediate. This difference in behaviour must be taken into account when modelling non-visual responses to light because it is probably not possible to generalize a single set of model parameters for non-visual responses.

The body of experimental evidence supporting the development of modelling the non-visual responses to light is growing. However, given that humans will move around frequently in realistic lighting environments, challenges associated with measuring human dynamic behaviour and biological response continue to be a barrier for developing design tools supporting the evaluation of non-visual responses to light in architectural settings. For a proof-of-concept, the HLR model was used to evaluate different annual daylight patterns to assess the influence of occupants' movements in a space (Amundadottir et al., 2013). The results demonstrate that by including predictions of occupants' movements in the evaluation, the non-visual efficiency of a space with access to a window is improved, compared to a stationary location and view direction. This is due to the temporal integration property of the HLR model, where intermittent light patterns are more effective than continuous light patterns.

## 6 Conclusion

Good lighting design has important beneficial effects both visually and biologically. It is important to advance research in this field to avoid design decisions that are based on an incomplete understanding of the underlying mechanism of the non-visual system. Light of certain wavelengths can have beneficial effects, but can also be harmful depending on the timing of the light exposure. Daytime light exposure can reduce sleepiness and improve performance; however, there is no agreement about the optimal daily light dose. Full-spectrum light stimulates visual and non-visual responses simultaneously and is therefore a good choice for daytime activities. At night, melanopsin-stimulating illuminance should be avoided, since it is known that light exposure can suppress melatonin production resulting in circadian disruption.

The long-term goal of this work is not to reveal the underlying mechanism of the non-visual system, but rather to establish a computational scheme that can be used to study and model human non-visual processing of light in order to evaluate different types of lighting conditions and rate their efficiency with respect to non-visual responses to light. For that reason, relatively simple models with few parameters were identified as most appropriate. The LNL model structure is considered to be one of the simplest nonlinear models. Such a model holds promise because its modular structure can be adapted as more experimental data becomes available. Further research is needed to refine and validate model predictions, and to assess the reliability and adequacy of the model to effectively inform design decisions. Ultimately, the proposed model may lead to new approaches for supporting healthy lighting design.

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