Retinal mesopic adaptation model for brightness perception under transient glare

Pablo Alejandro Barrionuevo,[1,*] Elisa Margarita Colombo,[1,2] and Luis Alberto Issolio[1,2]

[1]*Instituto de Investigación en Luz, Ambiente y Visión (ILAV), Consejo Nacional de Investigaciones Científicas y Técnicas—Universidad Nacional de Tucumán, Avda. Independencia 1800, San Miguel de Tucumán, 4000 Tucumán, Argentina*
[2]*Departamento de Luminotecnia, Luz y Visión, Universidad Nacional de Tucumán, Avda. Independencia 1800, San Miguel de Tucumán, 4000 Tucumán, Argentina*
**Corresponding author: pbarrionuevo@herrera.unt.edu.ar*

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A glare source in the visual field modifies the brightness of a test patch surrounded by a mesopic background. In this study, we investigated the effect of two levels of transient glare on brightness perception for several combinations of mesopic reference test luminances (Lts) and background luminances (Lbs). While brightness perception was affected by Lb, there were no appreciable effects for changes in the Lt. The highest brightness reduction was found for Lbs in the low mesopic range. Considering the main proposal that brightness can be inferred from contrast and the Lb sets the mesopic luminance adaptation, we hypothesized that contrast gain and retinal adaptation mechanisms would act when a transient glare source was present in the visual field. A physiology-based model that adequately fitted the present and previous results was developed.

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1. INTRODUCTION

The visual system uses two adaptation pathways to enable vision in a large range of environment luminances. The rod pathway responds to low luminances (scotopic range), whereas visual information processing is carried out by the cone pathway at high luminances (photopic range). The mesopic range is between the scotopic and photopic luminances and, in this range, both pathways work together. The limits of the mesopic range are not well established, but it has been suggested that mesopic luminance levels range from 0.001 cd/m^2 or 0.01 cd/m^2 to 3 cd/m^2 or 10 cd/m^2. Due to the fact that rod and cone pathways are different (spatially, temporally, and/or spectrally) and that their postreceptoral mechanisms interact with each other, visual system operations in the mesopic range are more complex than in the other domains [1–3].

From a behavioral point of view, an important argument in favor of studying mesopic vision is that light levels in this range are present in our daily activities. A good example of high demand in mesopic vision is night driving. In addition, the case in which strong light sources appear suddenly in the visual field, as in the case of oncoming automobiles, is of crucial importance [4].

It is well known that glare sources in the visual field can cause severe modifications in the perception of a scene. One of these modifications is an important reduction in the brightness of a stimulus surrounded by a dark background, whether it is steady [5] or transient [6]. In addition, glare increases contrast thresholds. This effect has been quantified by analyzing a veil of light overlapping the visual scene [7,8].

Concerning the influence of mesopic adaptation, Issolio and Colombo [9] showed the relevance of the luminance of the background on brightness perception under glare conditions. Contrarily, there was no effect when brightness evaluations were performed in photopic complex scenes in the presence of veiling luminances [10].

In Issolio and Colombo's study, the results were not fully explained by predictions based on the relation of luminances. A new hypothesis based on adaptation mechanisms in the mesopic range, however, could account for these results. Three decades ago, studies on detection thresholds showed evidence for the existence of subtractive and multiplicative adaptation mechanisms, either with cone or rod processing [11–14]. These mechanisms prevent saturation and in this way keep the system in a zone of linear performance. Also, physiological studies have shown changes in contrast gain for different levels of background luminance (Lb) [15].

Our hypothesis was that these mechanisms would act when a glare source was present in the visual field while processing brightness [16]. This hypothesis is supported by earlier works that showed the veil produced by glare caused the same effect as a light field that overlapped a stimulus [5,17]. Therefore, adaptation and contrast gain mechanisms could help to attenuate the glare effects.

In this study, we investigated the effect of transient glare on brightness perception for incremental stimuli (the test luminance [Lt] was always greater than the Lb) that were presented in different zones of the mesopic range of adaptation. In the first experiment, we tested the effect for several values of Lb. In order to evaluate the influence of adaptation and to analyze if our results were similar to those of Gilchrist and Jacobsen [10] with high mesopic conditions, we considered a wider range of Lbs than the range used by Issolio and Colombo [9]. In the second experiment, we tested the effect for several values of reference Lt. We considered two sets of Lts in different zones of the mesopic range. In this way, both experiments revealed the relative influence of the Lt and Lb. We also analyzed the data, taking into account two predictions based on the contrast and Lt, which finally led us to the proposal of a quantitative model. The model is composed of mechanisms of light adaptation, saturation, and contrast gain. When the model was applied, it explained the results and manner in which the responses of these mechanisms changed throughout the mesopic range.

2. METHODS AND SUBJECTS

We quantified brightness perception of incremental achromatic stimuli under two glare conditions using transient presentations.

A. Apparatus

Achromatic patterns were generated using a RGB framestore that was part of a purpose-built display controller, i.e., the Cambridge Research System's VSG2/3. The VSG 2/3 has two parallel operating palette chips. A higher resolution output was obtained by adding together the two palette outputs with different gains. This operating mode produced the effect of 12 bits of grey level resolution per pixel, which gave a more precise control of luminance. The stimulus was displayed on an Eizo T560i-T monitor. The monitor was gamma corrected over the luminance range used in the experiments, providing a luminance resolution of 0.01 cd/m^2.

The glare source was an incandescent lamp with intensity regulated by neutral density filters. The lamp was located 10° away from the line of sight at the same height as that of the test patch. An electronic shutter with an aperture of 1.5° controlled glare onset and offset. Figure 1 shows a diagram with the experimental layout.

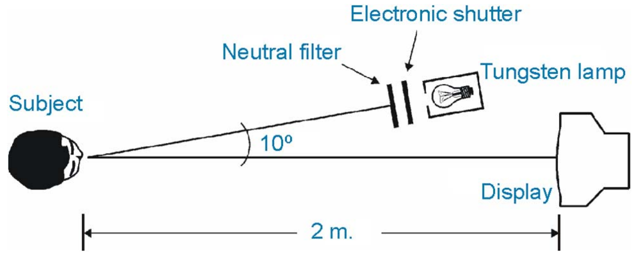

Fig. 1. Layout of the experimental design.

B. Stimuli

Stimuli were square patches of uniform luminance placed in the center of the monitor, subtending 1.2° at the cornea. The remaining area of the display (7° × 9.5°) was set to a Lb value (see stimuli conditions subsection) and the monitor was in a dark room at a viewing distance of 2 m. The CRT displayed two test patches sequentially (Fig. 2): a test with a comparison luminance (Lc) and an Lt (see stimuli conditions subsection). The Lc was equal to one of the six values determined in pilot sessions for each subject, for each glare condition, and for each Lt value.

A glare source was turned on simultaneously with the Lt and was kept on for 500 ms for each trial. The illuminances produced at a point between the two pupil centers were 60 and 30 lx. The stimuli were presented during a period of 300 ms with abrupt onset and offset. In this way, the Lt was viewed while the pupil was unaffected by glare [9,18]. The interstimuli interval was 1.2 s and the time between trials was 5 s in order to allow the pupil diameter to recover. The subject's response occurred after the presentation of the stimulus and was unlimited in time. Figure 2 shows the time course for the presentation of the stimuli and the glare source in a trial. Before each session, the subjects were given a 5 min period to adapt to the experimental conditions. In spite of the high level of illumination produced by the glare source, the short time that it was on produced a proportion of photo-pigment bleaching of 0.01% in the corresponding retinal area, which is a negligible value [19]. Glare illuminance was

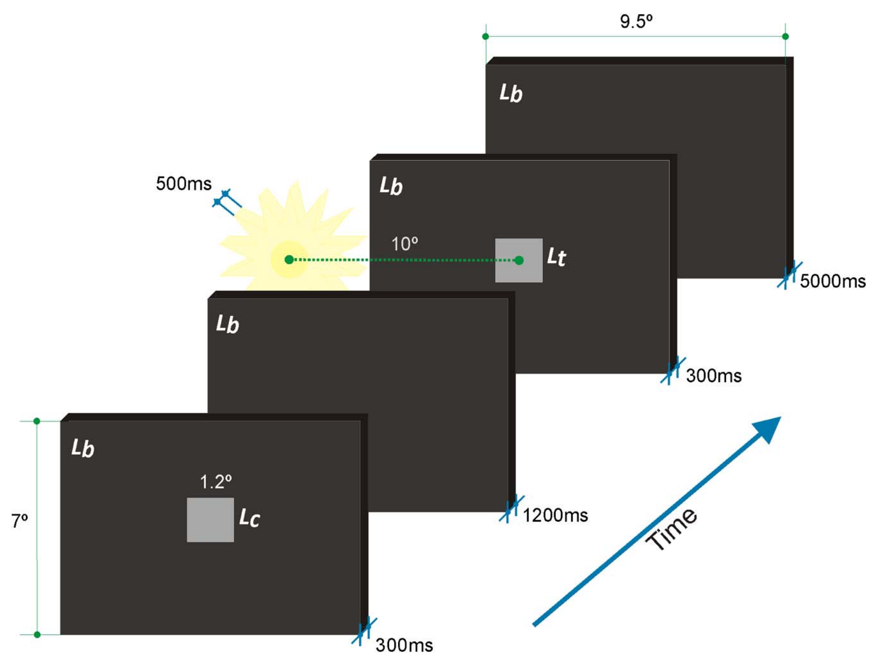

Fig. 2. Sequence of the stimuli for each trial.

measured with a Minolta T-1M illuminance meter and the stimulus luminance was measured with a LMT L1009 luminance meter.

C. Procedure

A 2IFC magnitude comparison paradigm was used with the constant stimuli method to obtain psychometric functions. There were two intervals in each trial. The Lc test was displayed in the first interval and the Lt was displayed simultaneously with glare in the second interval. The subject's task was to indicate which of the two patches appeared brighter by pressing a key. Twenty-six observations were completed for each value of Lc. The six Lc values were used in a randomized and balanced way. For each value of Lt, the experiment was repeated for the six pre chosen luminance values of Lc. We fitted logistic functions to the measured response distributions and found the point of subjective brightness equality or matching luminance (Lm) as the luminance value corresponding to a proportion of 0.5. Further explanation of the psychometric methodology can be found in Colombo *et al.* [6].

D. Stimuli Conditions

For the incremental stimuli tested (Lt > Lb), we analyzed the influences of the Lts and Lbs under different mesopic conditions considering different values of Lt and of Lb.

In the first experiment, we took into account two different fixed values of Lt (0.5 and 4 cd/m^2). For Lt = 0.5 cd/m^2, we considered eight different values of Lb (from low to intermediate in the mesopic range), and for Lt = 4 cd/m^2, we considered five other values of Lb (from intermediate to high in the mesopic range). These luminance values appear in Table 1.

For the second experiment, we assessed brightness perception for a fixed value of Lb equal to 0.01 cd/m^2 (the minimum luminance that we could set in our monitor), and for four values of Lt in the low mesopic range (Table 2). We also obtained a set of data fixing the Lb at 0.5 cd/m^2 using values of Lt in the high mesopic range (Table 2).

To choose the Lt and Lb values, we took into account that the stimuli were incremental and that the glare effects on brightness were to be studied in high and low mesopic luminance conditions (Fig. 3).

E. Subjects

In the first experiment, in which Lt = 0.5 cd/m^2, three young emmetropic subjects (MD, LI, and PB) carried out the task (25, 37, and 25 years old, respectively). The subject MD was naïve. When Lt was 4 cd/m^2, two additional young emmetropic subjects (AP, AD), plus one of the authors (PB), carried out the task (24, 24, and 29 years old, respectively). The subjects were naïve except for PB.

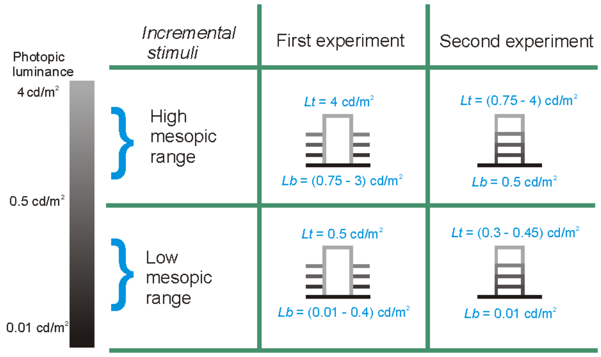

Fig. 3. Schematic diagram of the stimuli conditions for both experiments.

In the second experiment, when Lb was 0.01 cd/m^2, three young emmetropic subjects (AP, AD, and PB) carried out the task (24, 24, and 29 years old, respectively). The subjects were naïve except for PB. For Lb = 0.5 cd/m^2, three other young emmetropic subjects (IM, MC, and LI) carried out the task (29, 27, and 37 years old, respectively). The subjects were naïve except for LI.

3. RESULTS

A. First Experiment

Figure 4 shows Lms as a function of the Lb for three subjects. The Lm rose with an increase in the Lb, which was below the Lt for all subjects. For the three subjects, there was a systematic difference between the results obtained for 30 and 60 lx and this difference was almost zero for the highest Lb values. The glare effect was confirmed by a two-way ANOVA test that showed significant differences ($p < 0.01$).

When we represented the values of Lm as a function of Lb for three subjects at Lt = 4 cd/m^2 and for two glare levels (Fig. 5), there was no categorical evidence for brightness reduction. Slight variations were found in the data of AD and PB for 60 lx but the variations were in opposite directions. A one-way ANOVA test confirmed that for subjects AD and AP there was no significant difference between the two glare levels ($p > 0.05$). However, a slight difference was found ($p = 0.03$) for PB. The results obtained for Lbs in the higher mesopic range were different from those for Lbs in the lower mesopic range, since in the high range there was no systematic reduction in Lms; indeed there were some increases for some points (Fig. 5).

In order to analyze both sets of results together as a function of Lb, the results were normalized computing the Lm/Lt ratio and, for each glare illuminance, all the subjects' data

Table 1. Values of Luminance for the First Experiment

Lt (cd/m^2)	0.5								4				
Lb (cd/m^2)	0.01	0.025	0.05	0.075	0.1	0.15	0.2	0.4	0.75	1	1.5	2	3

Table 2. Values of Luminance for the Second Experiment

Lt(cd/m^2)	0.3	0.35	0.4	0.45	0.75	1	1.5	2	3	4
Lb(cd/m^2)	0.01				0.5					

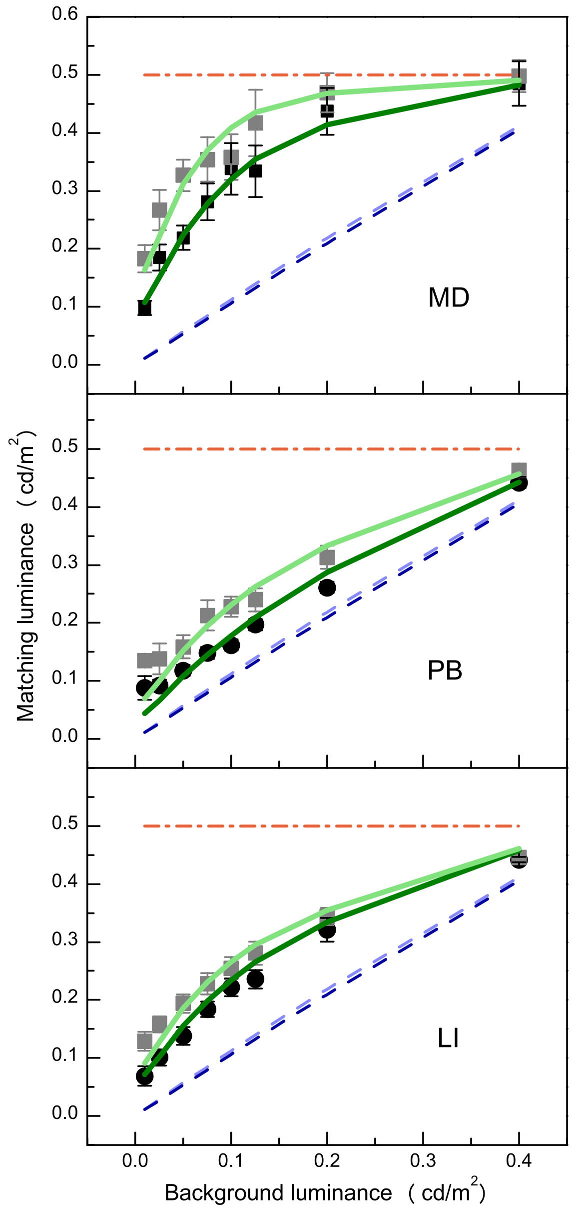

Fig. 4. Lms of the first experiment considering Lbs lower than Lt = 0.5 cd/m^2. The psychophysical results are represented by black circles for 60 lx of glare illuminance and by gray squares for 30 lx of glare illuminance. Solid lines represent the prediction of the model (light green for 30 lx and dark green for 60 lx). Dashed lines represent the contrast prediction (light blue for 30 lx and dark blue for 60 lx). A dash–dot line represents the Lt prediction. The results and predictions for each subject are shown in each panel.

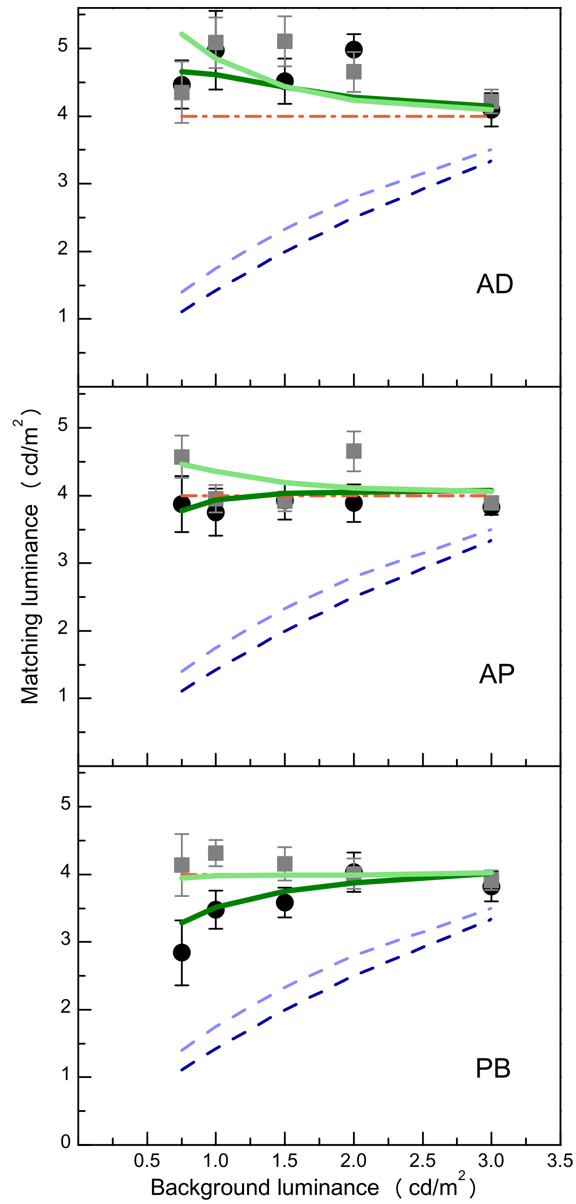

Fig. 5. Figure illustrates Lms for the first experiment considering Lts higher than 0.5 cd/m^2 (Lt = 4 cd/m^2). All the other considerations are similar to those of Fig. 4.

were averaged (Fig. 6). According to this figure, the relevant magnitude seems to be the Lb. Figure 6 shows that as the Lb increased, Lm/Lt also increased and reached a plateau. In the lower mesopic range there was a growing trend, while in the higher mesopic range, the Lm/Lt ratios were close to 1. Thus, brightness matching under glare conditions seems to be determined by different light adaptation processing in the mesopic range. The two glare levels produced significant differences in the results in a wide zone of the low mesopic range. For higher Lbs, there was no difference between the results for 30 and 60 lx. The strength of light adaptation (Fig. 6) was emphasized due to the fact that the Lb was maintained as constant during the experimental sessions.

B. Second Experiment

In the second experiment, we investigated the influence of the Lt values on brightness perception. Figure 7 shows Lm values as a function of Lt for the three subjects and the two glare levels for low Lbs. As we expected, a great reduction in brightness was found for all the glare and Lt combinations [6]. A slight increase in brightness could be attributed to the Lt level. It was confirmed by an ANOVA general linear model statistical test that considered the subject's glare level and Lt values as factors. A slightly significant difference was found for the Lt values tested ($F = 5.21$, $df = 3$, $p < 0.05$). The principal statistical differences were found between subjects ($F = 32.46$, $df = 2$, $p < 0.05$), and we did not find differences between the glare levels ($F = 0.81$, $df = 1$, $p = 0.38$).

Figure 7 also shows there were no clear differences between the effects of the two glare levels. For subjects PB

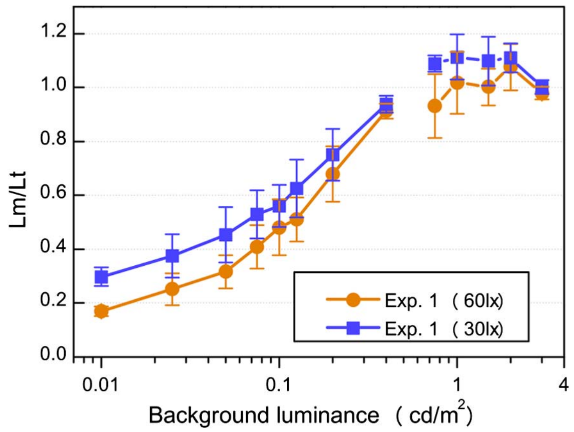

Fig. 6. Normalized mean results for the first experiment. The error bar is the standard error. The horizontal axis is in logarithmic scale for better appreciation.

and AD, a one-way ANOVA test confirmed that there was no difference between 30 and 60 lx. Subject AP was not able to carry out the task under 60 lx glare.

The reason for the overlap between the data for the two glare levels could be the magnitude of the Lt, which was insignificant in comparison with the two veiling luminances produced by glare. The task in this extreme condition became hard to carry out and the measurements became insensible. For this experiment, we concluded that changes in intermediate mesopic Lt values with low mesopic adaptation did not produce significant variations in brightness.

Figure 8 shows Lm values as a function of Lt for the three subjects and the two glare levels. The values of Lt (0.75–4 cd/m^2) belong to the high mesopic range. Lm increased as Lt increased for both glare levels considered. For LI, there was a minimal overestimation of brightness at some points, but for subjects MC and IM, brightness was

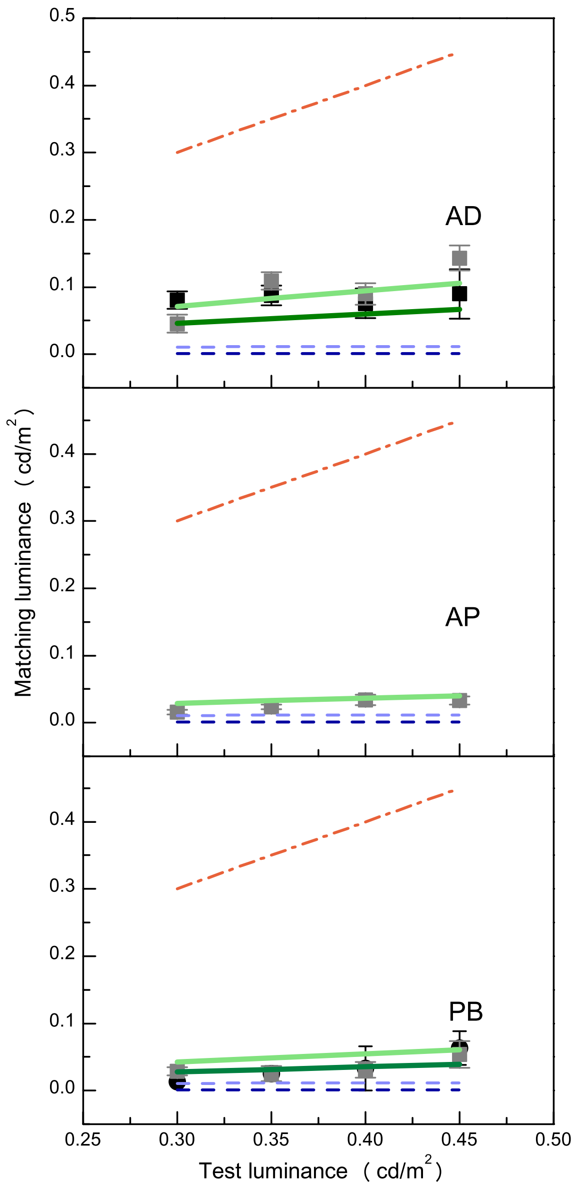

Fig. 7. Figure illustrates Lms for the second experiment considering Lts lower than 0.5 cd/m^2 with Lb = 0.01 cd/m^2. All the other considerations were similar to those of Fig. 4.

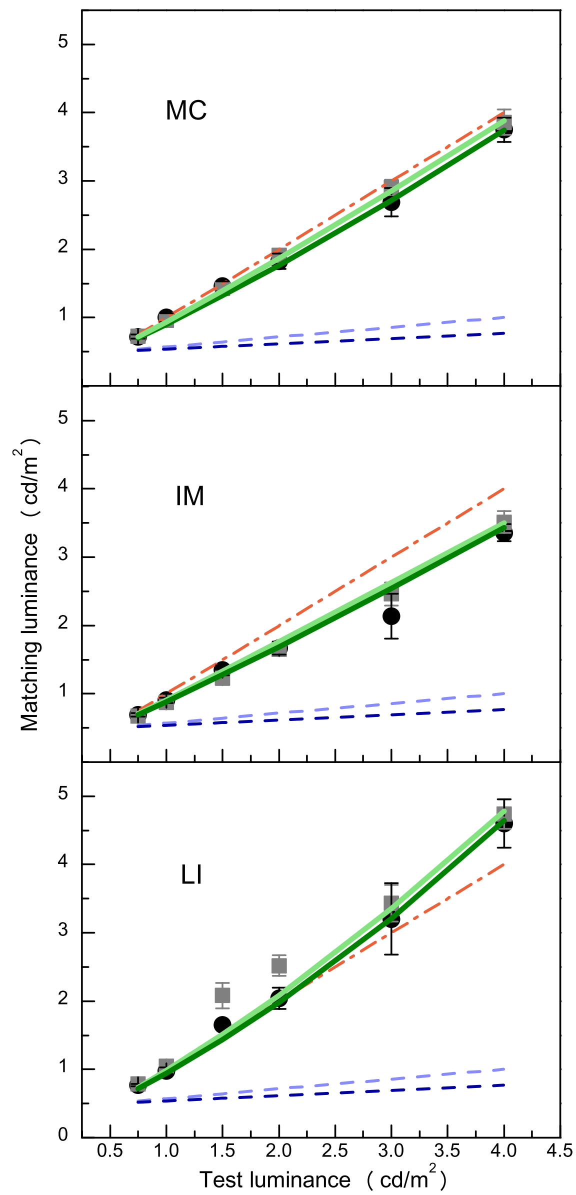

Fig. 8. Figure illustrates Lms of the second experiment considering Lts higher than the value of Lb (0.5 cd/m^2). All the other considerations were similar to those of Fig. 4.

slightly underestimated. Therefore, we concluded that there was no extra influence from the Lt on brightness perception.

An overlap between the data obtained for the two glare levels was also noticed, which indicated that the effect of these two different glare intensities on the brightness of the Lt was practically the same and was negligible. This was confirmed by an ANOVA test that showed no significant differences for the two glare levels ($p > 0.05$). Indeed, these results showed equivalence for nonglare and both glare conditions in the whole range of Lbs considered.

The Lb (0.5 cd/m^2) used for the results shown in Fig. 8 was about halfway through the mesopic range according to the background size [20]. The invariance of brightness was confirmed by the ratio $\mathrm{Lm/Lt} \approx 1$ for Lb values near 0.5 cd/m^2 (Fig. 6). Therefore, the weight of the Lb was evident in the results for the low to middle mesopic range. Considering the results from the second experiment, the influence of the Lt was weak.

4. PREDICTIONS AND PROPOSED MODEL

A. Lt and Contrast Predictions

In order to explain the data trends, we first proposed two predictions. The first and simplest prediction was under the hypothesis that matching was based on the Lt [Eq. (1)], which disregarded the glare effects. There is evidence that there are no modifications of brightness in photopic and high mesopic stimuli when brightness evaluations are performed in natural complex scenes in the presence of veiling luminances [10]. In Figs. 4, 5, 7, and 8, the dash–dot lines show the values of the Lt (Lt prediction).

$$\mathrm{Lm} = \mathrm{Lt}. \tag{1}$$

On the other hand, if only contrast matters in the matching of brightness, the contrast of the comparison test would be matched with the contrast of the reference patch under glare conditions [Eq. (2)],

$$\frac{\mathrm{Lm} - \mathrm{Lb}}{\mathrm{Lb}} = \frac{\mathrm{Lt} - \mathrm{Lb}}{\mathrm{Lb} + \mathrm{Lv}}, \tag{2}$$

where Lv is the veiling luminance computed for our glare conditions using the model [Eq. (3)] introduced by Holladay [7].

$$\mathrm{Lv} = k\frac{E}{\theta^2}, \tag{3}$$

where k is a constant that depends on the observer (equal to 10 for young subjects), E is the illuminance of the glare source, and θ is the angle between the glare source and the test patch.

We rearranged Eq. (2) to obtain Lms from this contrast prediction [Eq. (4)]. Dashed lines represent this hypothesis in Figs. 4, 5, 7, and 8:

$$\mathrm{Lm} = \left(\frac{(\mathrm{Lt} - \mathrm{Lb})}{\mathrm{Lb} + \mathrm{Lv}} + 1\right)\mathrm{Lb}. \tag{4}$$

Concerning the relation between data and predictions, the results of the first experiment for the low mesopic range (Fig. 4) were closer to the contrast prediction for the three subjects than to the Lt prediction. However, for all cases, the contrast prediction underestimated the results. In addition, the strong difference between the 30 and 60 lx data was not predicted by contrast matching. For the first experiment with stimuli luminances in the high mesopic range (Fig. 5), all the points were much closer to the Lt prediction than to the contrast prediction. Normalized mean results of this first experiment are shown in Fig. 6. In this graph, it is evident that the results obtained for the high mesopic condition showed a behavior that was different from those obtained for the low mesopic condition. In the second experiment, with low mesopic values of Lt and Lb (Fig. 7), the data were closer to, but underestimated by, the contrast prediction. For the data set with higher mesopic stimuli (Fig. 8), the results were closer to the Lt prediction; however, it did not account for differences between observers.

Neither the Lt nor the contrast predictions [Eqs. (1) and (2)] explained all the results, though each prediction accounted for some. Because of this, and on the basis that brightness can be inferred from contrast, we propose a model that adds particular characteristics of the visual system in the mesopic adaptation range.

B. Proposed Model

Shapley and Enroth-Cugell [21] claimed that the purpose of adaptation is to maintain the retinal response to contrast as invariant when illumination changes, thereby achieving a major goal, which is constancy of the visual perception of reflecting objects. This postulate seems to be demonstrated when considering some simple illusions in which two regions of equal luminance are seen to have different brightness when they are in different surroundings, such as in simultaneous brightness contrast [22], or when separated by two counterphase fine strips, which is called the Craik–O'Brian–Cornsweet effect [23].

Beginning with an analysis based on the equalization of contrasts, it is possible to predict the way in which the veiling luminance affects the brightness of stimuli surrounded by dark backgrounds. The darker the background, the more brightness is affected [Eq. (2)]. At the same time, as has been shown previously, for Lbs belonging to the high mesopic range, the data seem to follow the first prediction [Eq. (1)]. These two predictions are related to each other since, considering Eq. (4), when Lv is much lesser than Lb, this equation becomes $\mathrm{Lm} = \mathrm{Lt}$.

Based on the above, the Lm of the experiments that were carried out could depend on a comparison of contrasts. Although there is a reasonable approximation regarding the contrast prediction to the data (see Figs. 4 and 7), evidently this expression [Eq. (4)] is not enough to explain the behavior. Therefore, a model was developed that begins with the contrast prediction and takes into account retinal mechanisms, as well as their activity in the mesopic range.

C. Processing in the Mesopic Range

Given that the data to be modeled are in the mesopic range, it is important to establish which pathways are responsible for the processing of information. Cone signals in low light levels produce higher responses in parasol ganglion cells than in midget ganglion cells. This behavior is associated with the convergence benefit of parasol ganglion cells (magnocellular [MC] pathway) to integrate more signals for achieving a better signal–noise ratio [24]. Also, there is evidence that rod signals are transmitted predominately in the MC pathway [25]. Thus, the MC pathway in mesopic levels is a great protagonist for both rod and cone signals. Furthermore, physiological records from MC cells have shown that the contrast gain depends on the level of light adaptation [15,26]. Also, the MC pathway mediates the luminance channel [27], which is relevant due to our interest in brightness with achromatic stimuli. With the above considerations, in our model, we focused on processing in the MC pathway.

D. Model Structure

The mechanisms detailed below constitute the model presented in Fig. 9. According to the literature, these mechanisms for retinal adaptation have been widely developed and allow for a fairly complete description of the data on brightness perception under glare conditions. In the diagram, there are two pathways for processing, one for the signal that is derived from the test (foveal) and another for the signal from the background (parafoveal). The veiling luminance covers the entire retina, which is why both pathways are involved. The foveal and parafoveal signals are processed independently by adaptation and saturation mechanisms. Then, to process the contrast, both signals are combined and affected by the contrast gain mechanism. Finally, the combined signal is sent to thalamic and cortical centers to produce brightness perception.

E. Nonlinearity (Saturation)

The cells of the retina have a response range of two orders of magnitude while the dynamic range of light intensities in real-world scenes may exceed 8 orders of magnitude. To deal with this fact, the system presents a nonlinear response. Traditionally, this response has been characterized with a hyperbolic equation [13,21,28], commonly expressed as

$$R[I] = \frac{I^n}{I^n + \sigma^n} R_{\max}, \tag{5}$$

where R is the response of the cell, I is the stimulation of the cell, σ is the constant of semi-saturation, n is an exponent that describes the relation between the amount of the response and the stimulation, and $R_{\max}$ is the maximum response of the cell. Equation (5) describes the function intensity response of a cell. It is approximately linear when I is much lesser than σ. The system response is saturated when the stimulation is greater than σ and, therefore, any increment of I provokes only a small change in R. In our case, the retina is adapted to low Lbs and, when the glare source is turned on, the retina receives strong light stimulation (L) that can saturate the response of the cells. For modeling purposes, we assigned this mechanism to the ganglion cells. Assuming that, during a first transduction stage, the relation between I and L is linear, so that $I = pL$ where p is a constant of proportionality and assuming also that p is equal to 1, $I = L$, so that Eq. (2) is best expressed as follows:

$$\frac{R[\mathrm{Lm}] - R[\mathrm{Lb}]}{R[\mathrm{Lb}]} = \frac{R[\mathrm{Lt} + \mathrm{Lv}] - R[\mathrm{Lb} + \mathrm{Lv}]}{R[\mathrm{Lb} + \mathrm{Lv}]}. \tag{6}$$

F. Light Adaptation

The objective of the adaptation mechanism is to prevent saturation of the cell responses. The mechanism can be either multiplicative or subtractive. A multiplicative system produces the effect of multiplying the stimuli luminances by a factor without producing changes in the contrast, acting as an automatic gain control. In this way, after receiving a large amount of light, the retinal gain is reduced so that the neural response does not usually saturate in the physiological range of illumination [21].

Mechanisms of this type have been suggested as acting in rod pathways [13] and in cone pathways [11,12]. In the case of rod pathways, with low illumination, the signals are processed by the retina following the pathway of bipolar rod cells, and the place of adaptation is found in the synaptic connection between bipolar rod cells and AII amacrine cells. The time required for adaptation is approximately a few hundred milliseconds [29]. For the cone pathways, two sites of multiplicative adaptation were identified. The first is in the same photoreceptor and responds to high levels of light (greater than 10 $\mathrm{cd/m^2}$), while the second is located in the synaptic connection between the bipolar and ganglion cells. These two mechanisms do not act together; they are mutually exclusive. Both mechanisms are fast and, therefore, adequate when working in a period of time that demands visual fixation [24]. Hayhoe *et al.* [14] considered that this performance could be produced in periods of approximately 50 ms. Given the aforementioned adaptation multiplicative characteristics, this type of mechanism would affect all the factors of Eq. (1)

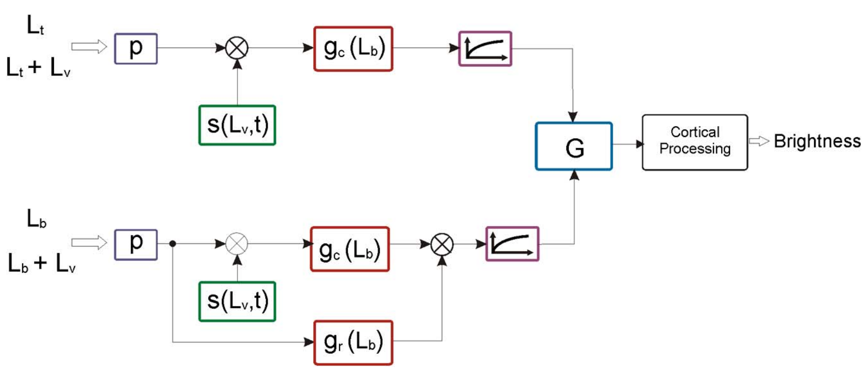

Fig. 9. Diagram of the model structure.

equally and would act prior to saturation [14]. We can generically identify this mechanism as "g" and incorporate it into Eq. (6). This would result in a new contrast comparison, as follows:

$$\frac{R[g\mathrm{Lm}] - R[g\mathrm{Lb}]}{R[g\mathrm{Lb}]} = \frac{R[g'\mathrm{Lt} + g'\mathrm{Lv}] - R[g'\mathrm{Lb} + g'\mathrm{Lv}]}{R[g'\mathrm{Lb} + g'\mathrm{Lv}]}, \quad (7)$$

where factors g and g' represent the effect of a multiplicative mechanism without glare and with glare, respectively. As the presentation of our stimulus was 300 ms and the presence of glare was 500 ms, we assumed that the multiplicative mechanisms had already acted. The subtractive mechanisms partially or totally eliminate the signal corresponding to steady luminance, reducing this to a lower effective value. In this way, they attempt to recover the dynamic range of the cells that are involved. Initially, the subtractive signal is nonexistent but it increases with time and tends to remove the stable background signals [13]. For the cone pathway, a mechanism has been proposed whose response becomes slower as the increment of luminance becomes larger [30]. It has been suggested that this mechanism takes place in horizontal cells that are modulated through a feedback circuit from amacrine cells via interplexiform cells [31]. A mechanism of this type is incorporated into the model in the following manner:

$$\frac{R[g\mathrm{Lm}] - R[g\mathrm{Lb}]}{R[g\mathrm{Lb}]} = \frac{R[g'\mathrm{Lt} + g'\mathrm{Lv} - g's] - R[g'\mathrm{Lb} + g'\mathrm{Lv} - g's]}{R[g'\mathrm{Lb} + g'\mathrm{Lv} - g's]}, \quad (8)$$

where s represents the effect of the subtractive mechanism when glare is present. Similar to multiplicative mechanisms, the value of s depends on the state of adaptation. Associated with this mechanism, there is a parameter (τ) that is present in the differential equation for the subtractive mechanism (s), shown in Table 3 [particularly concerning Eq. (A3) in Appendix A].

G. Contrast Gain

One of the main hypotheses of the model is that brightness perception is computed from retinal contrast information, and glare affects retinal contrast. On the other hand, glare changes the retinal illumination. It is well known that retinal contrast gain mechanisms are dependent on the illumination [15,21]; therefore, this type of mechanism must be included in the proposed model as follows:

$$G\left(\frac{R[g\mathrm{Lm}] - R[g\mathrm{Lb}]}{R[g\mathrm{Lb}]}\right) = G'\left(\frac{R[g'\mathrm{Lt} + g'\mathrm{Lv}] - R[g'\mathrm{Lb} + g'\mathrm{Lv}]}{R[g'\mathrm{Lb} + g'\mathrm{Lv}]}\right), \quad (9)$$

where factors G and G' express the effect of the contrast gain mechanism without and with glare, respectively. Measurements carried out on the ganglion cells of macaques indicated that mechanisms of this type are found in the retina and that the value of gain increases with the level of adaptation [15,26]. Associated with this mechanism, there is a factor (k_G) that indicates the state of adaptation to contrast during the time in which the stimulus is present {Table 3, Appendix A [particularly in Eq. (A9) to compute G]}.

The prediction of Lm, taking into account the various mechanisms mentioned above, is expressed in Eq. (10). In Appendix A, we described the implementation of the following model:

$$\mathrm{Lm} = \frac{\sigma/g}{\left(\frac{1}{Rm} - 1\right)^{1/n}};$$
$$Rm = \left(\frac{G}{G'}\left(\frac{R[g'\mathrm{Lt} + g'\mathrm{Lv} - g's]}{R[g'\mathrm{Lb} + g'\mathrm{Lv} - g's]} - 1\right) + 1\right)R[g\mathrm{Lb}]. \quad (10)$$

H. Application of the Model to the Data

Most of the parameters that appear in the model are fixed (see Appendix B). One parameter that varies, depending on the glare condition and the subject, is intraocular scattering [32,33]. In our model, this quantity was computed following the CIE equation [33] and it set the value of Lv (Table 3). The other variable parameter corresponds to the subtractive mechanism (τ). It was optimized for each subject and, as it did not vary with the stimuli conditions, this parameter was intrinsic to the subject (Table 3). We considered that this parameter encompasses the between-subject differences in the time course of rapid processing of adaptation. From Table 3, it can be seen that τ depends on the subject, although there is no direct relation with some of the individual characteristics such as age (this could be due to the fact that all the subjects are young). All the values were between 85 and 150 ms, which is a range that contains the value (140 ms) estimated by Wilson [31]. The model has a totally free parameter that

Table 3. Values of the Veiling Luminance (Lv) Computed for Each Glare Level and Each Subject[a]

Experiment	Subject	E (lx)	Lv (cd/m^2)	τ (sec)	k_G
First (Lt = 0.5 cd/m^2)	LI	30	2.17	*0.085*	*0.45*
		60	4.35		
	PB	30	1.67	*0.15*	*0.78*
		60	3.34		
	MD	30	1.66	*0.085*	*0.7*
		60	3.31		
First (Lt = 4 cd/m^2)	PB	30	1.69	*0.15*	*0.95*
		60	3.38		
	AP	30	1.84	*0.13*	*0.95*
		60	3.69		
	AD	30	2.02	*0.11*	*0.94*
		60	4.05		
Second (Lb = 0.01 cd/m^2)	PB	30	1.69	*0.15*	*0.75*
		60	3.38		
	AP	30	1.84	*0.13*	*0.4*
		60	3.69		
	AD	30	2.02	*0.11*	*0.97*
		60	4.05		
Second (Lb = 0.5 cd/m^2)	LI	30	2.17	*0.085*	*0.67*
		60	4.35		
	IM	30	1.71	*0.09*	*0.6*
		60	3.42		
	MC	30	1.86	*0.09*	*0.65*
		60	3.72		

[a]The values of the optimized parameters (in italics) used for the model fits (Figs. 4, 5, 7, and 8) are shown. Note: the difference between the Lv values for PB was due to the fact that the measurements were made in different years.

corresponds to the contrast gain mechanism (k_G). This parameter seems to depend on the extrinsic and intrinsic adaptation conditions as, generally speaking, its value increased with the increase in Lt for subjects AP, PB, and LI (see differences between experiments in Table 3), and it is possible to consider a contrast gain process with a different time course for each subject. In these experiments, the values of k_G were between 0.4 and 0.97. Since this factor is lower than 1, the value of G' is closer to G, which could mean that the adaptation to the new contrast set considering Lv was not completely attained.

The fits of the model appear in Figs. 4, 5, 7, and 8 and are represented by solid lines. In all cases, the model describes the form of the different groups of data better than the contrast and luminance predictions for the test. In addition, the fits accounted for the results at different orders of magnitude, which gave robustness to the model. The model is sufficiently adequate for representing the variability among the subjects. It is also remarkable that, for a combination of Lt and Lb, the difference between the trends for the two glare levels was only determined by the computation of Lv.

I. Application of the Model to Decremental Data

Experiments with transient glare, taking into account both incremental and decremental (Lb higher than the luminance of the test) stimuli, were carried out by Issolio and Colombo [9]. They used a glare source with an illuminance of 60 lx, Lt = 0.5 cd/m^2, and Lb from 0.01 cd/m^2 to 2 cd/m^2. The results of this study are reproduced in Fig. 10 together with the predictions of the model. In a similar way to Experiment 1, the incremental stimuli (Lb less than 0.5 cd/m^2) showed a behavior that could be approximately explained with the prediction of contrast (Fig. 4). However, for decrements (Lb larger than 0.5 cd/m^2), Lm flattened up a bit below Lt, strongly differing from the contrast prediction and becoming closer to the luminance prediction [9]. Using the proposed model in the present work, the data of Issolio and Colombo were fitted quite well. In this way, and by means of retinal mechanisms, it is possible to explain both incremental and decremental stimuli, also confirming that the model is robust.

5. DISCUSSION

We tested the effect of transient glare on brightness perception for several combinations of mesopic Lts and Lbs. At the lowest level of Lb, we confirmed the highest reduction in brightness as reported by a previous study [6]. As we increased Lb, a growing trend was consistent with the findings of Issolio and Colombo [9]. The present work adds evidence that, for a high mesopic range, there is no major brightness variation and, therefore, glare effects can be discounted in this light range. Furthermore, these new results show that variation of the Lt does not produce significant differences in the expected Lm.

The proposed model was adequate in explaining the effects of glare for various levels of brightness, which was the objective of this work. It was also successful in fitting previously reported decremental data [9]. Comparing the fit of the model with the contrast prediction and Lt prediction, the model yielded a better fit and took into account the particularities of each subject.

In the low mesopic range, the reduction in brightness was consistent with a reduction in performance of other visual tasks, such as reaction time and achromatic threshold, due to the adaptation level diminishing [34,35] and the addition of glare in the scene [36]. In the high mesopic range, brightness invariance resembled the behavior found in complex, real-world scenes for photopic levels [10].

Shapley and Enroth-Cugell [21] stated that one of the main objectives of the visual system is to achieve constancy in the visual perception of reflecting objects, using the calculation of contrast as a strategy. Brightness reduction in our experiments was partially explained with the approach represented in Eq. (2). On the other hand, light adaptation has been traditionally studied by evaluating contrast thresholds. However, it has been claimed that adaptation mechanisms could also process brightness [16,21] and lightness [37]. In addition, early works have shown that the addition of a veiling luminance acts as a step-up in the Lb [17,38]. These considerations, together with Lb dependence on both adaptation and contrast gain mechanisms [15,24,29], were implemented in the proposed model.

Our model allowed us to show that both the reduction in brightness observed in the low zone of the mesopic range and the invariance of brightness observed in the high zone of the mesopic range can be the consequences of the behavior of light adaptation and contrast gain mechanisms that affect the processing of contrast. An analysis of the relative participation of these mechanisms revealed that both kinds of mechanisms (contrast gain and light adaptation) are necessary to account for the results.

In the data of the first experiment for the lower mesopic luminances (Fig. 4), the adequate fit of the model was due mostly to the effect of the adaptation mechanisms that varied with the level of retinal luminance. At the same time, it is remarkable that the differences between glare levels can be fitted by the model by only changing the Lv values, calculated using the equation recommended by the CIE [33] and

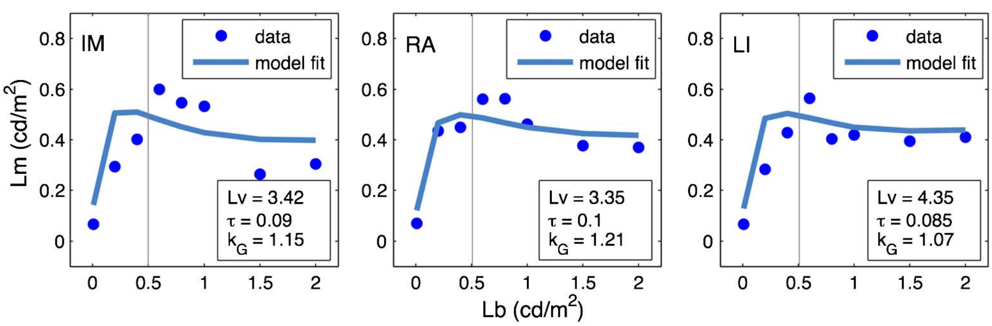

Fig. 10. Model fits for the data of Issolio and Colombo (2006), considering incremental (Lb < 0.5 cd/m^2) and decremental (Lb > 0.5 cd/m^2) stimuli.

determined for each subject according to age and iris color. The differences between observers can be attributed to the variation of the time constant of the subtractive mechanism, which was optimized for each subject. With respect to the data for the higher mesopic luminances from the first experiment (Fig. 5), the prediction of the Lt behaved very well. However, the model yielded a better fit and the subtractive mechanism, which strongly reduced the effect of Lv, was mainly responsible for this. The lack of effectiveness of the subtractive mechanism in low luminances could be due to the fact that, for lower mesopic luminances, the processing was dominated by rods and their adaptation mechanisms are different in relation to cone mechanisms.

Considering that the rationale of the second experiment was to analyze the influence of Lt (Fig. 8), we found that Lm was practically the same as Lt for Lbs in the middle zone of the mesopic range. However, in the case of Lbs in the lower zone of the mesopic range (Fig. 7), brightness was strongly reduced for all considered values of Lt. Therefore, we conclude that, from the point of view of adaptation, the results of the second experiment can be explained using the same mechanisms that explained the results of the first experiment.

Previous models for general adaptation conditions have been quite successful in explaining changes in the sensitivity of the visual system, assigning physiological correlations to light adaptation mechanisms [31,39] and incorporating contrast gain mechanisms [40], as has been done in the present work. However, previous studies have not explicitly dealt with brightness. In addition, the present work has the particularity of incorporating physiological evidence regarding the relationship of these mechanisms with the Lb [15,24,29] and dealing specifically with visual system function in the mesopic range.

The Stiles–Crawford effect is higher for cones than for rods and, therefore, one could assume that rods are affected more by glare. However, rods could be affected in a similar way to cones if rod directional sensitivity is ultimately found to be narrower than expected for dipole molecules [41]. In any case, the relation between glare and the Stiles–Crawford effect in rods and cones is not clear.

Some measurements carried out on the visual cortex showed that the processing of brightness is carried out by cells belonging to V1 [42,43]. Also, computational models that deal with brightness illusions are in favor of the early visual cortex [44–46]. In this work, local processing had great relevance, since the effects of glare were explained in terms of adaptation mechanisms, while any interaction that might exist between the signal responding to the foveal stimulus and that resulting from the distal retinal image of the glare source was considered unimportant. A hypothesis based on this interaction was considered in the work of Issolio *et al.* [47]. However, in this study, we were able to achieve a much wider description of the results that took into account a variety of conditions for the Lt and Lb.

It would be interesting to evaluate the model prediction with transient Lbs instead of glare. If we sequentially present a comparison test with a dark background and a Lt with a transient Lb (both tests with the same luminance value), the comparison test should be brighter than the Lt, as in the case of contrast induction. The model prediction is a reduction in the brightness of the Lt, because the transient nature of the background will activate the model mechanisms in a similar way to transient glare. In the case of steady glare, studies have shown that a brightness reduction exists for a dark background, which is not as strong as for the transient case [5,48]. Although for practical purposes it is possible to establish a relation between transient luminance and steady glare [49], the current work adds evidence that for particular conditions (as transient glare), besides intraocular scattering (Lv), neural activity also takes part in the processing [50,51].

APPENDIX A: APPLICATION OF THE MODEL TO OUR EXPERIMENTAL CONDITIONS

In our experiments, the presentation of the 1.2° test was foveal, which is a zone that is free of rods [52]. The test light, therefore, was exclusively stimulating the cone pathway. However, the background light stimulated the parafovea containing cones and rods. For this reason, we used specific mechanisms of the cone pathway for processing the Lt, while mechanisms acting on both cones and rods were used for processing of the Lb (Fig. 9).

To explain how the multiplicative process depends on cone illumination, a representative logarithmical function was incorporated into the model, taking into consideration the data provided by Dunn *et al.* [24] for parasol cells. According to this data, the registers for parasol cells showed that they adapt to minor luminance changes better than midget cells. For parasol cells, when the background level increases, the width of the response decreases. In this way, the value of g depends on Lb and the value of g' is a function of the stable value of the Lb plus the transitory component (Lv) because the mechanism is quick (50 ms).

For the region of the test, the system adapted alternately to the background and to the test, which is why adaptation in the fovea differed from adaptation in the periphery. For the rod pathway, the response of the multiplicative mechanism depended on the Lb. This dependency was characterized following a rational function that was employed in the work of Dunn *et al.* [29] [i.e., Eq. (5) of that paper with parameter values for gain in primate ganglion cells).

There is evidence that combination of the signals of cones and rods occurs prior to saturation [26]. This combination (I_{comb}) can be modeled by means of a linear relationship [53] of the type

$$I_{\mathrm{comb}} = I_c x + I_r(1 - x), \tag{A1}$$

where I_c and I_r are stimulations of cones and rods, respectively, and x is a function that depends on the level of luminance adaptation

$$x = \frac{\mathrm{Lb}^m}{\mathrm{Lb}^m + \alpha}, \tag{A2}$$

where α and m are two parameters that determine the change of concavity and the slope of the curve, respectively [53].

According to Hayhoe *et al.* [30], implementation of the subtractive mechanism implies that it is dependent both on time and on the luminance increment produced, which, in our case, was equal to Lv. Therefore, the effect of the subtractive mechanism can be modeled by a differential equation [31] of the following type:

$$\frac{ds}{dt} + \frac{g_m}{\tau} s = C \frac{g_m}{\tau}, \qquad (A3)$$

in which τ is the time constant, g_m is the factor that modifies the speed of the mechanism so as to reach a stable state, and C is a factor that depends on the transient peripheral stimulation. Therefore

$$C = k_s \mathrm{Lv}, \qquad (A4)$$

where k_s is a constant of proportionality. The value of g_m in Eq. (A3) depends on Lv, which represents the increment of luminance. Wilson [31] considered a similar mechanism and proposed the following equation to compute the value of g_m:

$$g_m = 0.5 + 0.0664 IP. \qquad (A5)$$

In our case, we were interested in the response for a 300 ms presentation time of the test. Following Hayhoe's reasoning, the subtractive response becomes slower as the increment of luminance becomes larger [30]. It can be assumed that IP is proportional to the stimulation

$$IP = k_f I, \qquad (A6)$$

where k_f is a proportionality constant that would integrate the intermediate processing between the direct pathway and feedback by means of interplexiform cells, and I would be the response of the system to Lv, after the multiplicative adaptation, so that Eq. (A5) would stand as follows:

$$g_m = 0.5 + 0.0664 k_f g' \mathrm{Lv}. \qquad (A7)$$

The contrast gain increases with the value of retinal luminance [15]. For this reason, the values of G and G' are different as they depend on the quantity of light that reaches the eye which, in the case of G', is $\mathrm{Lb} + \mathrm{Lv}$ and, in the case of G, is Lb. We estimated the values of G and G' for each retinal illumination based on the data of Purpura *et al.* [15] for M-cells:

$$G[\mathrm{Lb}] = -0.97 + 0.72 \ln[\mathrm{Lb} + 4.25], \qquad (A8)$$

where Lb is expressed in Td. On the other hand, there is evidence that contrast adaptation times are a few seconds [54] and, since our stimulus is presented during 300 ms, the system would not fully adapt to the contrast imposed by Lt and Lv. Following this reasoning, we added a factor (k_G) to compute G':

$$G' = k_G G[\mathrm{Lb} + \mathrm{Lv}]. \qquad (A9)$$

In this way, this factor (k_G) would indicate the state of adaptation to contrast for the time that the stimulus lasts.

APPENDIX B: MODEL PARAMETERS

The saturation mechanism has two parameters: σ and n, with σ fixed at 0.5, which is approximately the value used by Hayhoe *et al.* [14], and n fixed at 1, as recommended in previous works [13,14]. The subtractive mechanism parameters k_s and k_f were both fixed at 1. The parameter τ was left free to explain the differences between subjects. The parameters α and m model the combination of cone and rod signals in the periphery. According to Sagawa [53], they were fixed at $\alpha = 0.05$ and $m = 1$. Lv was determined by the level of intraocular scattering. The intraocular scattering depends on the age and color of pigmentation of the iris of the subject, as well as the opacities of the lens [32,33]. Bearing in mind that all the subjects were young and without any kind of ocular illness, the value of Lv was estimated according to the CIE equation [33], which considers all these factors. Factor k_G was left as a free parameter.

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REFERENCES

1. B. M. Matesanz, L. A. Issolio, I. Arranz, C. de la Rosa, J. A. Menéndez, S. Mar, and J. A. Aparicio, "Temporal retinal sensitivity in mesopic adaptation," Ophthalmic Physiolog. Opt. **31**, 615–624 (2011).
2. A. Reeves, "Visual adaptation," in *The Visual Neurosciences*, L. Chalupa and J. Werner, eds. (MIT, 2004) pp. 851–862.
3. A. Stockman and L. T. Sharpe, "Into the twilight zone: the complexities of mesopic vision and luminous efficiency," Ophthalmic Physiolog. Opt. **26**, 225–239 (2006).
4. I. C. Bichao, D. Yager, and J. Meng, "Disability glare: effects of temporal characteristics of the glare source and of the visual-field location of the test stimulus," J. Opt. Soc. Am. A **12**, 2252–2258 (1995).
5. G. A. Fry and M. Alpern, "The effect of a peripheral glare source upon the apparent brightness of an object," J. Opt. Soc. Am. **43**, 189–195 (1953).
6. E. M. Colombo, J. F. Barraza, and L. A. Issolio, "Effect of brief exposure to glare on brightness perception in the scotopic–mesopic range," Light. Res. Technol. **32**, 65–69 (2000).
7. L. L. Holladay, "Action of a light-source in the field of view in lowering visibility," J. Opt. Soc. Am. **14**, 1–15 (1927).
8. D. C. Hood and M. A. Finkelstein, "Sensitivity to light," in *Handbook of Perception and Human Performance: Sensory Processes and Perception*, K. Boff and L. Kaufman, eds. Vol. **1** (Wiley, 1986) pp. 5-1–5-66.
9. L. A. Issolio and E. M. Colombo, "Brightness for different surround conditions: the effect of transient glare," Percept. Psychophys. **68**, 702–709 (2006).
10. A. L. Gilchrist and A. Jacobsen, "Lightness constancy through a veiling luminance," J. Exp. Psychol. Hum. Percept. Perform. **9**, 936–944 (1983).
11. W. Geisler, "Adaptation, afterimages, and cone saturation," Vis. Res. **18**, 279–289 (1978).
12. D. C. Hood, T. Ilves, and E. Maurer, "Human cone saturation as a function of ambient intensity: a test of models of shifts in the dynamic range," Vis. Res. **18**, 983–993 (1978).
13. E. Adelson, "Saturation and adaptation in the rod system," Vis. Res. **22**, 1299–1312 (1982).
14. M. Hayhoe, N. Benimoff, and D. Hood, "The time-course of multiplicative and subtractive adaptation process," Vis. Res. **27**, 1981–1996 (1987).
15. K. Purpura, E. Kaplan, and R. M. Shapley, "Background light and the contrast gain of primate P and M retinal ganglion cells," Proc. Natl. Acad. Sci. USA **85**, 4534–4537 (1988).

16. P. Whittle and P. D. C. Challands, "The effect of background luminance on the brightness of flashes," Vis. Res. **9**, 1095–1110 (1969).
17. R. M. Boynton, W. Rush, and J. M. Enoch, "Rapid changes in foveal sensitivity resulting from direct and indirect adapting stimuli," J. Opt. Soc. Am. **44**, 56–60 (1954).
18. E. M. Colombo, S. A. Comastri, L. A. Issolio, and R. Echarri, "Pupil light reflex produced by glare under mesopic adaptation," J. Light Visual Environ. **31**, 70–79 (2007).
19. C. B. Blakemore and W. A. Rushton, "Dark adaptation and increment threshold in a rod monochromat," J. Physiol. **181**, 612–628 (1965).
20. S. Raphael and D. I. A. MacLeod, "Mesopic luminance assessed with minimum motion photometry," J. Vis. **11**(9), 14 (2011).
21. R. Shapley and C. Enroth-Cugell, "Visual adaptation and retinal gain controls," in *Progress in Retinal Research*, N. N. Osborne and G. J. Chader, eds., Vol. **3** (Pergamon, 1984), pp. 263–346.
22. A. L. Gilchrist, *Seeing Black and White* (Oxford University, 2006), pp. 3–124.
23. T. N. Cornsweet, *Visual Perception.* (Academic, 1970), p. 273.
24. F. A. Dunn, M. J. Lankheet, and F. Rieke, "Light adaptation in cone vision involves switching between receptor and post-receptor sites," Nature **449**, 603–606 (2007).
25. B. B. Lee, V. C. Smith, J. Pokorny, and J. Kremers, "Rod inputs to macaque ganglion cells," Vis. Res. **37**, 2813–2828 (1997).
26. D. Cao, B. B. Lee, and H. Sun, "Combination of rod and cone inputs in parasol ganglion cells of the magnocellular pathway," J. Vis. **10**(11), 4 (2010).
27. B. B. Lee, J. Pokorny, V. C. Smith, P. R. Martin, and A. Valberg, "Luminance and chromatic modulation sensitivity of macaque ganglion cells and human observers," J. Opt. Soc. Am. A **7**, 2223–2236 (1990).
28. K. I. Naka and W. A. H. Rushton, "S-potentials from colour units in the retina of fish (cyprinidae)," J. Physiol. **185**, 536–555 (1966).
29. F. A. Dunn, T. Doan, A. P. Sampath, and F. Rieke, "Controlling the gain of rod-mediated signals in the mammalian retina," J. Neurosci. **26**, 3959–3970 (2006).
30. M. M. Hayhoe, M. E. Levin, and R. J. Koshel, "Subtractive processes in light adaptation," Vis. Res. **32**, 323–333 (1992).
31. H. R. Wilson, "A neural model of foveal light adaptation and afterimage formation," Vis. Neurosci. **14**, 403–423 (1997).
32. D. P. Piñero, D. Ortiz, and J. L. Alio, "Ocular scattering," Optom. Vis. Sci. **87**, E682–E696 (2010).
33. J. J. Vos, B. L. Cole, H. W. Bodmann, E. M. Colombo, T. Taekuchi, and T. J. T. P. Van Den Berg, CIE 146:2002 CIE equations for disability glare, Technical Report (Commission Internationale de L'Eclairage, 2002).
34. M. Eloholma, J. Ketomäki, P. Orreveteläinen, and L. Halonen, "Visual performance in night-time driving conditions," Ophthalmic Physiolog. Opt. **26**, 254–263 (2006).
35. D. Cao, A. J. Zele, and J. Pokorny, "Linking impulse response functions to reaction time: rod and cone reaction time data and a computational model," Vis. Res. **47**, 1060–1074 (2007).
36. R. C. Aguirre, E. M. Colombo, and J. F. Barraza, "Effect of glare on simple reaction time," J. Opt. Soc. Am. A **25**, 1790–1798 (2008).
37. A. Radonjić, S. R. Allred, A. L. Gilchrist, and D. H. Brainard, "The dynamic range of human lightness perception," Curr. Biol. **21**, 1931–1936 (2011).
38. W. A. Rushton and R. W. Gubisch, "Glare: its measurement by cone thresholds and by the bleaching of cone pigments," J. Opt. Soc. Am. **56**, 104–110 (1966).
39. S. Shah and M. D. Levine, "Visual information processing in primate cone pathways. I. A model," IEEE Trans. Syst. Man Cybern. B **26**, 259–274 (1996).
40. H. P. Snippe, L. Poot, and J. H. van Hateren, "A temporal model for early vision that explains detection thresholds for light pulses on flickering backgrounds," Vis. Neurosci. **17**, 449–462 (2000).
41. G. Westheimer, "Directional sensitivity of the retina: 75 years of Stiles–Crawford effect," Proc. Biol. Sci. **275**, 2777–2786 (2008).
42. M. Kinoshita and H. Komatsu, "Neural representation of the luminance and brightness of a uniform surface in the macaque primary visual cortex," J. Neurophysiol. **86**, 2559–2570 (2001).
43. A. F. Rossi and M. A. Paradiso, "Temporal limits of brightness induction and mechanisms of brightness perception," Vis. Res. **36**, 1391–1398 (1996).
44. B. Blakeslee and M. E. McCourt, "A multiscale spatial filtering account of the White effect, simultaneous brightness contrast and grating induction," Vis. Res. **39**, 4361–4377 (1999).
45. X. Otazu, M. Vanrell, and C. Alejandro Párraga, "Multiresolution wavelet framework models brightness induction effects," Vis. Res. **48**, 733–751 (2008).
46. A. E. Robinson, P. S. Hammon, and V. R. de Sa, "Explaining brightness illusions using spatial filtering and local response normalization," Vis. Res. **47**, 1631–1644 (2007).
47. L. A. Issolio, J. F. Barraza, and E. M. Colombo, "Time course of brightness under transient glare condition," J. Opt. Soc. Am. A **23**, 233–238 (2006).
48. P. A. Barrionuevo, E. M. Colombo, M. Vilaseca, J. Pujol, and L. A. Issolio, "Comparison between an objective and a psychophysical method for the evaluation of intraocular light scattering," J. Opt. Soc. Am. A **29**, 1293–1299 (2012).
49. L. A. Issolio, P. A. Barrionuevo, S. A. Comastri, and E. M. Colombo, "Veiling luminance as a descriptor of brightness reduction caused by transient glare," J. Opt. Soc. Am. A **29**, 2230–2236 (2012).
50. J. Schouten and L. Ornstein, "Measurements on direct and indirect adaptation by means of binocular vision," J. Opt. Soc. Am. **29**, 168–192 (1939).
51. D. Schreuder, *Outdoor Lighting: Physics, Vision, and Perception.* (Springer, 2008), pp. 286–311.
52. G. Osterberg, *Topography of the Layer of Rods and Cones in the Human Retina* (Nyt Nordisk Forlag, 1935), pp. 1–103.
53. K. Sagawa, "Toward a CIE supplementary system of photometry: brightness at any level including mesopic vision," Ophthalmic Physiolog. Opt. **26**, 240–245 (2006).
54. K. J. Kim and F. Rieke, "Temporal contrast adaptation in the input and output signals of salamander retinal ganglion cells," J. Neurosci. **21**, 287–299 (2001).