



## Temporal retinal sensitivity in mesopic adaptation

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### Abstract

**Purpose:** Night driving is a complex visual task with important ramifications for driver and pedestrian safety. It is usually performed under mesopic or scotopic conditions and frequently, in the presence of transient glare sources that can adapt parts of the central retina. The objective of this work was to analyze the time response of adaptation for the central 15° of the retina when part of it is exposed to transient or steady mesopic adapting fields.

**Methods:** Absolute visual thresholds and luminance thresholds when viewing steady and transient adaptation fields were measured for three observers, at temporal retinal eccentricities of 0°–14.5° in steps of 2.9° (subsequently described as 0°, 3°, 6°, 9°, 12° and 15°) using a two-channel Maxwellian view optical system. The adaptation field and stimulus subtended 1.05° and 0.45° respectively. The transient adaptation field was presented with a stimulus onset asymmetry (SOA) of 300 ms. Time course adaptation curves were also measured at 0°, 6° and 9°.

**Results:** The absolute dark adaptation threshold (threshold measured at dark adaptation conditions or  $L_t^d$ ) decreases in peripheral retina due to an increasing rod contribution. Luminance thresholds vs eccentricity curves for transient ( $L_t^{SOA300}$ ) and steady ( $L_t^{LA}$ ) mesopic adaptation fields intersect across the first 15° of the peripheral retina.

**Conclusions:** While the fovea shows higher sensitivity than the areas of peripheral retina investigated in this study, the speed of adaptation, measured from the visibility loss, is greater for retinal regions between 6° and 9° than for the fovea or retinal eccentricities beyond 9°.

### Introduction

Driving a vehicle is an important daily activity that requires substantial involvement of the visual system.<sup>1</sup> For example, the visual conditions under which night driving is carried out involve low lighting levels ranging from the scotopic to the mesopic range,<sup>2,3</sup> and objects need to be identified both foveally and more peripherally. All this implies the simultaneous involvement of both cone and rod functions. The night driving task is also characterized by the presence of dazzling sources that reduce the contrast of the object and the brightness of the scene. Moreover, these dazzling sources generally present a transient

characteristic that forces the system to continuously change the state of adaptation.

In the past, the luminance thresholds obtained under conditions of transient adaptation were compared to those obtained with steady fields, and it was observed that a transient field produces a greater loss of retinal sensitivity than a steady one, both for extrafoveal vision<sup>4–6</sup> and for foveal vision in a photopic range of adaptation.<sup>7,8</sup> However, under adaptation conditions at a mesopic level, Geisler<sup>4</sup> found that at an eccentricity of 5° the retinal sensitivity loss caused by a transient adaptation is the same as that produced by a steady condition. This result, as well as others obtained under mesopic lighting

conditions,<sup>9–12</sup> showed that, for certain ranges of luminance and at certain retinal locations, the global contribution of rods and cones to the adaptation process might be different to that observed when studying only the behaviour of cones, as is the case for photopic adaptation levels.

The fovea plays a fundamental role, but peripheral vision is also important since it helps detect and locate objects or events of interest that can be potentially dangerous. Several authors have paid special attention to the ability and speed of adaptation at different retinal eccentricities. For example, the retinal temporal recovery in photopic lighting conditions in the presence of direct glare has been measured by Bodmann *et al.*<sup>13</sup> The results showed that there is an important loss of visibility at the fovea, which is reduced at 5° but increases again for greater eccentricities. Moreover, Bichao *et al.*<sup>14</sup> studied the effect of a transient indirect glare in the photopic range on foveal and eccentric stimulus detection, finding that the effects of transient glare are greater in the periphery than in fovea. Since these last two studies were performed under different experimental conditions and using different measurement paradigms, comparisons between them are difficult. As a result, it is impossible to predict the behaviour of the retinal periphery in a transient adaptation condition. Recently, Plainis *et al.*<sup>15</sup> measured luminance thresholds during slow adaptation processes in the mesopic range for two different eccentricities. It was noted that the recovery speed of photopigment regeneration is greater for adaptation at high mesopic levels and that the rate of recovery decreases as eccentricity increases, but there remains a need to study the fast processes of adaptation.

When mesopic lighting conditions are considered, the different levels of saturation, spatial distributions and rates of adaptation of rods and cones generate an interaction which changes throughout the mesopic range.<sup>16</sup> The dominant photoreceptor type depends upon several factors, such as the spectral composition of the test, the luminance level of the field and the retinal location of the stimulus. While most studies examining the time course of retinal adaptation have focused on the recovery time or reaction time,<sup>17,18</sup> there is a gap in current understanding about the ability and speed of adaptation of the retina in the detection of mesopic stimuli under dazzling conditions.

## Methods

### Subjects

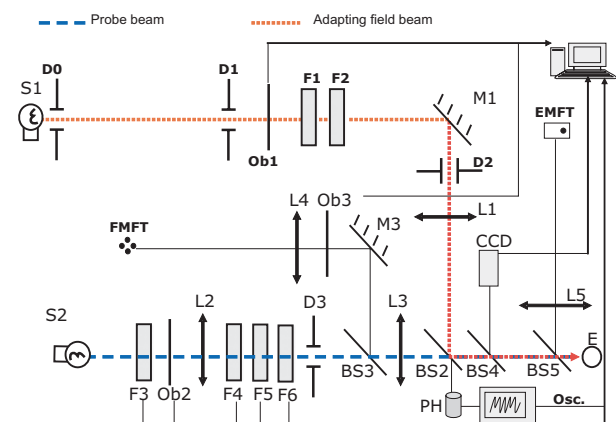
Three authors (IA, BM and CR aged 38, 40 and 24 years respectively) served as observers for the study. They were ocularly healthy, as certified by an optometric

examination, which included ophthalmoscopy and slit-lamp biomicroscopy. Subjective refraction was performed to obtain optimal visual acuity (at least 0.0 logMAR, Snellen equivalent 6/6 in all cases) and appropriate trial case lenses were used in all experiments.

### Experimental arrangement

The experimental set-up, illustrated in *Figure 1*, is a two-channel Maxwellian view optical system. Two incandescent halogen 50 W lamps (S1 and S2), emitting at a colour temperature of 3000 K, were employed, connected to independent and stabilized power supplies. Lenses L2 and L3, placed in the probe beam (marked in dashed line in *Figure 1*), and lens L1, placed in the adapting field beam (marked in dotted line in *Figure 1*) image S2 and S1 filaments, respectively, onto the plane of the eye's entrance pupil E, as well as the circular field stops D3 and D2 at optical infinity. The angular size of these probe and adapting fields was 0.45° and 1.05°, respectively. Several rotating disks F containing neutral density filters were placed in both beams, permitting the control of the light level entering the eye in steps of 0.1 log units. Luminance was measured with a Spectra Pritchard model 1980A luminance meter placed in the position occupied later by the observers and focused at the planes containing diaphragms D2 and D3, i.e. optical infinity.

The temporal features of both stimuli were controlled by electronic Uniblitz shutter systems Ob1, Ob2 ([www.uniblitz.com](http://www.uniblitz.com)), with a temporal uncertainty in stimulus duration or delay between stimulus onsets of <1 ms. These temporal parameters were measured by means of the photodiode (PH), connected to an oscilloscope. As in other foveal and extrafoveal experiments,<sup>4,5,19</sup> probe field duration was 40 ms for both foveal and extrafoveal



**Figure 1.** Experimental arrangement.

measurements. This also allowed direct comparisons between results from both parts of the retina.

Foveal measurement fixation test (FMFT) and extrafoveal measurement fixation test (EMFT) were generated by tiny light emitting diodes (LEDs, central wavelengths at 630 nm) imaged at optical infinity by lenses L4 and L3 for the FMFT and L5 for the EMFT, respectively. FMFT consisted of four dim red fixation points in a diamond configuration with horizontal and vertical dimensions of 0.45° in order to avoid unsteady fixation.<sup>20</sup> EMFT consisted of a single dim red point which could be displaced in a perpendicular direction to the L5 optical axis in order to induce foveal fixation with measurements on extrafoveal locations up to approximately 15° of eccentricity. These LEDs subtended less than six min from the observer's pupil. This was also illuminated by eight infrared LEDs (central wavelength at 830 nm), in such a way that a CCD camera, incorporating a filter blocking the visible light, was used to monitor the pupil at all times. The observer stabilized her head by biting on a bite bar, which had an impression of her teeth in a dental compound. This was placed on a XYZ positioning system. This whole monitoring system enabled the pupil to be centred on S1 and S2 image filaments, which were previously overlapped, and to minimize the Stiles–Crawford effect. Rotating disks F, shutters Ob, the CCD camera and the oscilloscope, which received the photodiode signal, were controlled from the experiment computer.

**Procedure**

For all observers, the right eye was employed while the left eye was occluded. As a first step, careful positioning of the observer's pupil was made on the plane and position where the S1 and S2 image filaments previously overlapped. Fine adjustments of XY positioning in D2, D3 and FMFT locations were made so that the observers could detect the circular probe and adapting beams as concentric and centred on FMFT. EMFT was also centred on FMFT prior to extrafoveal measurements. In foveal measurements (EMFT switched off) subjects were instructed to fixate the centre of the FMFT. In extrafoveal measurements (FMFT switched off) the subject fixated on the EMFT displaced from the L5 optical axis in such a way that the adapting and probe beams fell on the desired part of the temporal retina for their right eye. The temporal retina was selected due to its high sensitivity.<sup>21</sup> Retinal locations from 0° to 14.5° were considered in steps of 2.9°. Subsequently, these are simplified to 0° (fovea), 3°, 6°, 9°, 12° and 15°.

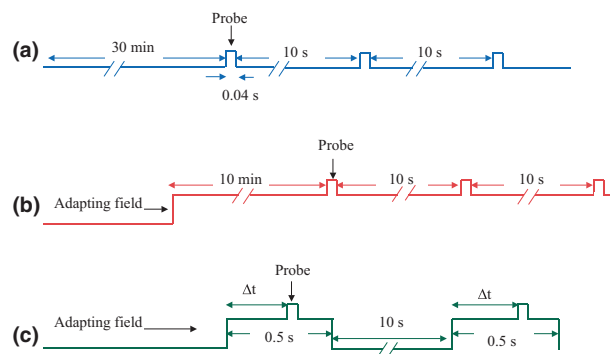
The observers were always dark adapted for at least 30 min before any session. The luminance of the observer's field of view was lower than  $5 \times 10^{-6}$  cd m<sup>-2</sup>. In

order to determine luminance detection threshold, the following procedure was used. For any adapting field condition considered, a preliminary threshold value for the probe beam was obtained by the method of limits. Five luminance levels of the probe, in steps of either 0.1 or 0.2 log units for 9°, 12° and 15° eccentricities, were selected around this preliminary value. After that, a method of constant stimuli was used, with 20 measurements at each of the five selected probe luminance levels. Probe luminance levels were randomly ordered in this test sequence. The observer's task on each trial was to report whether the probe was visible or not. The differences between threshold luminance values obtained by the method of limits and the method of constant stimuli were always lower than 0.15 log units.

Two experiments were performed. In the first one, luminance thresholds at the fovea and 3°, 6°, 9°, 12°, and 15° of the peripheral retina were measured at (1) dark adaptation DA (shutter Ob1 continuously closed, *Figure 2a*); (2) steady light adaptation (shutter Ob1 continuously opened, *Figure 2b*); and (3) transient light adaptation condition with a fixed stimulus onset asynchronies of 300 ms (SOA300, the probe was presented 300 ms after the onset of the adapting field which lasts for 500 ms, *Figure 2c*). The probe and adapting field were flashed every 10 s.

In the second experiment, luminance thresholds were measured in transient light adaptation conditions with SOA varied (SOA = -25, 0, 50, 150, and 300 ms) at the fovea and 6° and 9° eccentricities, in order to determine the time course adaptation at each of these eccentricities (*Figure 2c*).

In both experiments, the adapting field luminance was 5 cd m<sup>-2</sup>, a typical luminance condition in night driving<sup>15</sup> and very close to the upper limit of the mesopic



**Figure 2.** (a) Sequence for dark adapting condition (b) sequence for steady light adapting condition (c) sequence for transient light adapting condition with  $\Delta t$  ms delay between beginning of the adapting field and probe. In conditions (b) and (c), adapting field was 5 cd m<sup>-2</sup>.

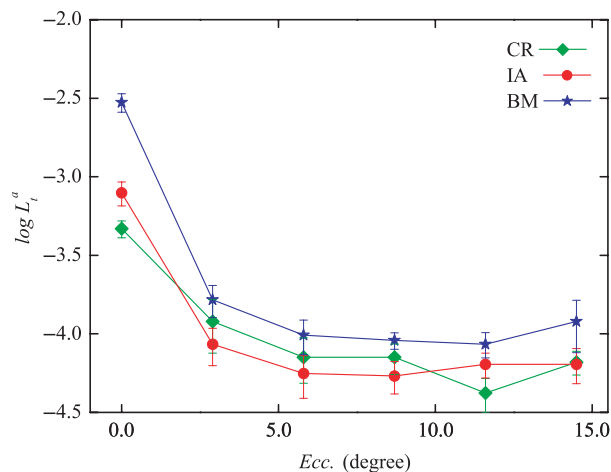
range proposed by CIE.<sup>22</sup> The natural pupil was always employed since the pupil diameter during miosis, due to light exposure in steady and transient adaptation, proved to be greater than S1 and S2 image filaments. In other words, the effect of pupil variations on retinal illumination due to pupil miosis can be considered negligible in this experiment. This also allowed us to employ (photopic)  $\text{cd m}^{-2}$  units for all further threshold measurements.

**Results**

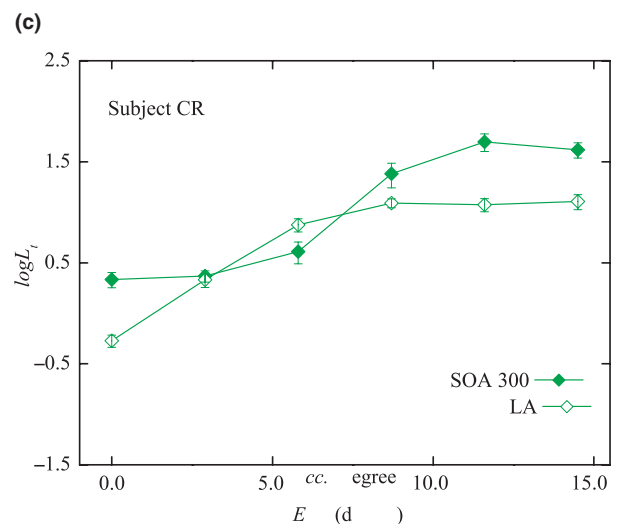
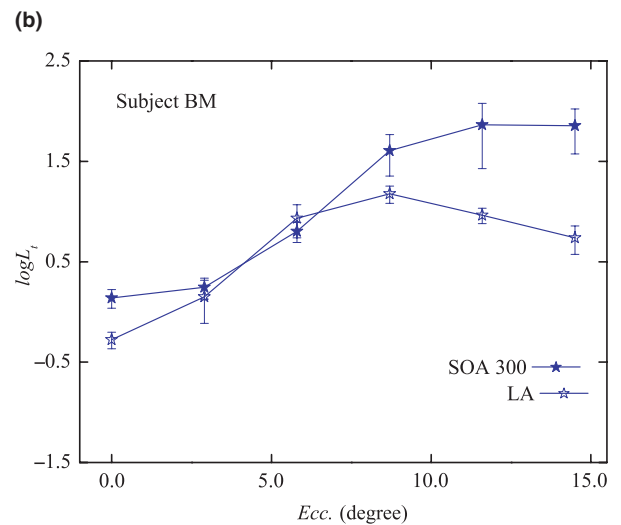
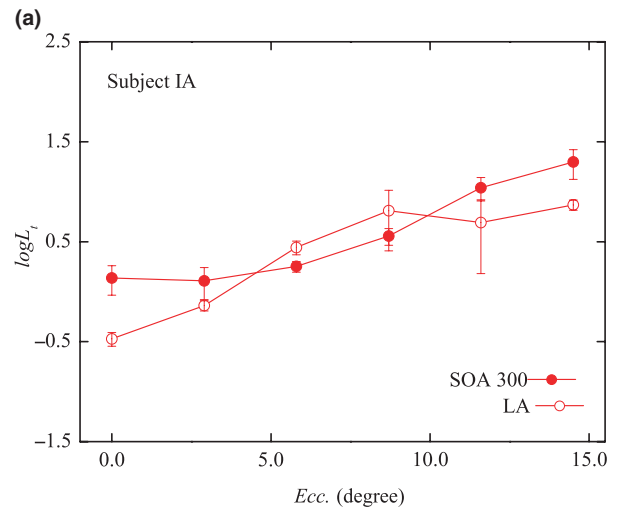
When the method of constant stimuli was employed, the luminance for a correct response rate of 50% correct was determined from fitting the data with a logistic function. This fitting procedure was sufficient in all cases, as indicated by non-significant ( $p > 0.05$ ) chi-squared values. The 25% and 75% detection levels obtained from these fits were used as the error bar associated with each threshold.

**Experiment 1. Dark adaptation, steady light adaptation and transient adaptation**

In Figure 3 absolute luminance thresholds  $L_t^a$  (in  $\text{cd m}^{-2}$ ) are represented in log units as a function of eccentricity for all subjects. These values correspond to measurements performed under dark adaptation conditions. As shown in this figure, these absolute thresholds are similar for the three observers in all retinal locations. They decrease from a maximum at the fovea towards the periphery and may reflect the increased spatial summation of rod signals in the periphery.



**Figure 3.** Absolute luminance thresholds measured in dark adaptation conditions.

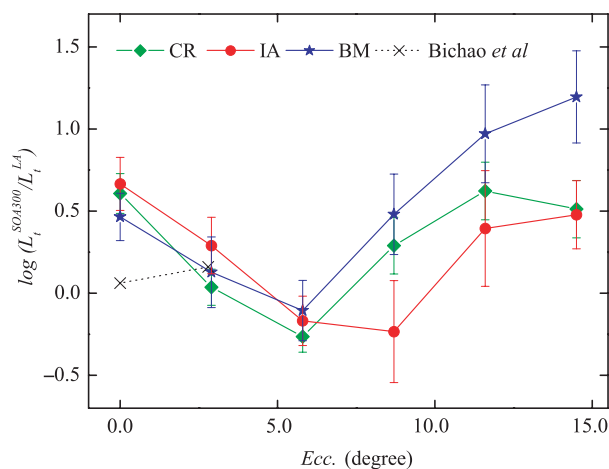


**Figure 4.** Luminance thresholds for each subject, measured in steady light and transient (SOA300) adaptation conditions.

Figure 4a–c show luminance thresholds  $L_t$  (in  $\text{cd m}^{-2}$ ) in log units measured in steady and transient light adaptation (SOA = 300 ms) conditions as a function of eccentricity for each subject. The threshold for the steady light adaptation condition increased continuously from the fovea to  $9^\circ$  in all cases. When comparing these with the results of Figure 3, we can see a very different functional trend. In dark adaptation conditions, the test is shown against no background, while in steady light adaptation or transient adaptation conditions the test is shown against a mesopic background ( $5 \text{ cd m}^{-2}$ ). Figure 3 reflects a behaviour mainly governed by rods, while Figure 4 shows a behaviour mainly (but perhaps not exclusively) governed by cones.

As shown in Figure 4,  $L_t^{\text{SOA300}}$  and  $L_t^{\text{LA}}$  curves intersect in one or two places around  $6^\circ$  or  $9^\circ$  eccentricity for all observers, with  $L_t^{\text{SOA300}}$  above  $L_t^{\text{LA}}$  for peripheral locations lower than  $6^\circ$  and higher than  $9^\circ$ . These results indicate that the peripheral retinal areas around the fovea ( $6^\circ$ – $9^\circ$ ) seem to show a faster adaptation process than the fovea when they are exposed to a transient mesopic adapting flash.

In order to quantify this effect, we have chosen the ratio  $\phi = L_t^{\text{LA}}/L_t^{\text{SOA300}}$  as an index. This is the inverse of the commonly known *sensitivity loss*. When this index is close to unity (or its log is close to zero) it indicates that adaptation was achieved in a period of time as short as 300 ms. Lower or larger values indicate that sensitivity has already been recovered or not yet respectively. In Figure 5 we include these measurements of the log of sensitivity loss for all measured eccentricities. As can be seen, the log sensitivity loss vs retinal eccentricity curve shows similar behaviour for all observers. In all cases, the



**Figure 5.** Log sensitivity losses for retinal locations up to  $15^\circ$  eccentricity. Data from Bichao *et al.* experiment for SOA500 have also been included (points joined by a dotted line).

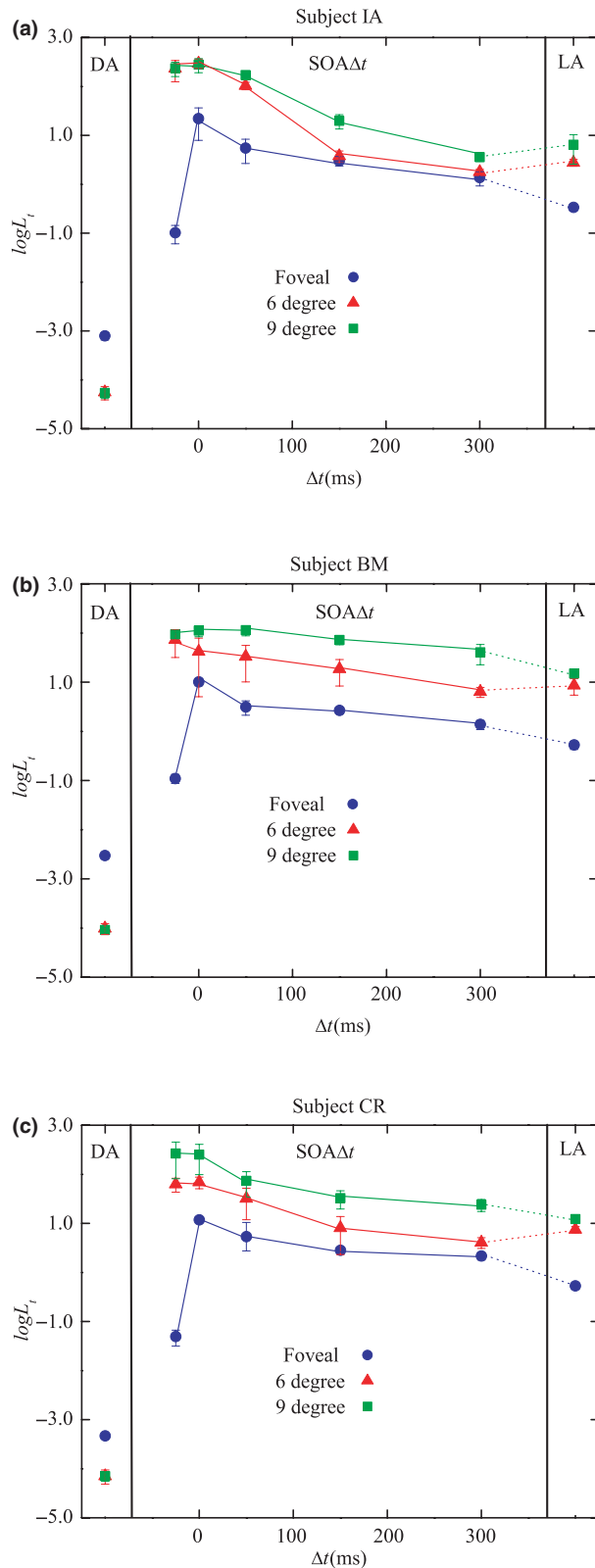
$\log(1/\phi)$  tends to decrease from the fovea to the near periphery (up to  $6^\circ$  or  $9^\circ$  depending on observers) and then increases for greater eccentricities. This U-shape shows that the speed of adaptation increases with eccentricity up to  $6^\circ$  or  $9^\circ$  and then decreases. In addition, data from Bichao *et al.*<sup>14</sup> were also included. They were measured in the fovea and at an eccentricity of  $2.8^\circ$ . The authors calculated the index with the threshold luminances obtained at an SOA of 500 ms. Thus, our results clearly indicate that there is a retinal area, between  $3^\circ$  and  $9^\circ$ , where complete adaptation is achieved in 300 ms while closer to the fovea and eccentricities greater than  $9^\circ$  need more time to recover complete sensitivity.

### Experiment 2. The time course of adaptation

Figure 6a–c show the results, for the three observers, of the log luminance thresholds (in  $\text{cd m}^{-2}$ ) measured at different asynchronies (SOA $\Delta t$ ), at fovea,  $6^\circ$  and  $9^\circ$ . This figure also contains the  $L_t^a$  and  $L_t^{\text{LA}}$  values shown in Figures 3 and 4 for these eccentricities. These curves inform us, not only about the sensitivity of these different retinal locations at this mesopic adapting level, but also of their different speeds in adapting to it. As shown in this figure, sensitivity changes in a similar way for the three observers at these three eccentricities. For all of them, the luminance threshold increases significantly even for  $\Delta t = -25$  ms, that is, when the probe beam is presented prior to the onset of the adapting beam. This effect is particularly substantial for the peripheral retinal locations. In all cases, foveal luminance thresholds rise quickly, reaching their maximum values at  $\Delta t = 0$  ms, when probe and adapting field onsets are simultaneous. Afterwards, they fall and tend to reach the  $L_t^{\text{LA}}$ -value ( $\Delta t = \infty$ ). Although similar behaviour is observed in peripheral retina, adaptation appears faster for  $6^\circ$  and  $9^\circ$ .

As can be seen in Figure 6, 300 ms after the onset of the adapting field,  $L_t^{\text{SOA300}}$  is lower than  $L_t^{\text{LA}}$  at  $6^\circ$  eccentricity for the three observers (positive slope of the dotted lines). This indicates that the adaptation process has ended. This situation is opposite to that found at the fovea, for which  $L_t^{\text{SOA300}}$  is greater than  $L_t^{\text{LA}}$  (negative slope of the dotted lines). This indicates that the adaptation process has not yet concluded. At  $9^\circ$  eccentricity, subject IA shows a different behaviour than that of subjects BM or CR. In the first case, adaptation was completed at 300 ms while it had not ended for the other two observers.

In order to consider all the information contained in the adaptation curves measured in this second experiment, we have fitted the time course evolution curves shown in Figure 6 with decreasing exponential functions  $\log L_t(t) = a + be^{-ct}$  being  $a = \log L_t^{\text{LA}}$  the asymptotic



**Figure 6.** Time course adaptation at fovea, 6° and 9° of eccentricity for the three subjects.

**Table 1.** Parameters  $1/c$  (ms) of the luminance thresholds evolution during the adaptation to a mesopic transient field of  $5 \text{ cd m}^{-2}$  for the three observers and at the three eccentricities considered in Experiment 2

Subject	Fovea	6° ecc.	9° ecc.
IA	256	71	116
BM	263	135	435
CR	333	71	147

threshold value which is obtained under steady adaptation and  $c$  the time constant which informs us about the speed of adaptation. Table 1 shows the  $1/c$ -parameters in ms for the three observers and for the three eccentricities considered. In these calculations, data obtained at an SOA of  $-25 \text{ ms}$  have been excluded. As can clearly be seen in this table, the inverse of time constants for all subjects are lower at  $6^\circ$  eccentricity than at the fovea or at  $9^\circ$ . This result again confirms the greater speed of adaptation in the peripheral retina that was highlighted earlier.

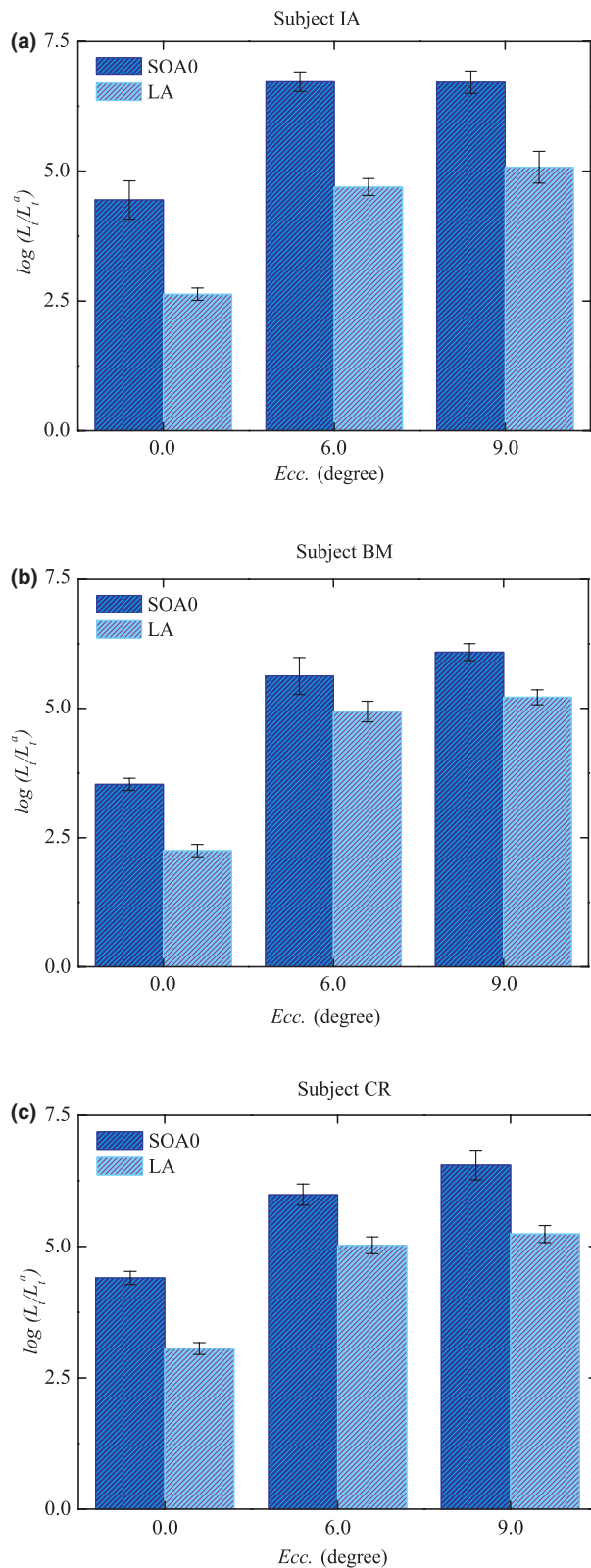
Further evidence of a faster speed of adaptation in the retinal periphery close to  $6^\circ$  or  $9^\circ$  can also be seen in this figure. Luminance thresholds measured an SOA of  $-25 \text{ ms}$  for  $6^\circ$  or  $9^\circ$  are higher than those obtained at the fovea. Furthermore, at these eccentricities, they are close to those obtained with no SOA. This effect, known as *backward masking*,<sup>23</sup> has been explained by assuming that the time required by the visual system to transmit information to the brain regarding a flash is inversely proportional to the luminance of the flash.<sup>24</sup> From this point of view, Figure 6 informs us that, an SOA of  $-25 \text{ ms}$ , *backward masking* is much greater when the test and adaptation fields are located in retinal locations between  $6^\circ$  and  $9^\circ$  than when they are located at the fovea. Finally, it is also important to state that the measured  $L_t^{\text{SOA}300}$ -values should not be affected by the threshold masking due to the flash offset, since this flash lasts for 500 ms and background masking, if it occurs, exists only in the few milliseconds prior to the background offset.

In conclusion, for these mesopic conditions, time course adaptation curves are functionally different. This seems to indicate that different retinal locations show a different ability to adapt to changes from darkness to a mesopic light level.

**Sensitivity loss with transient and steady light adapting fields**

The next question we faced in this work was to assess detection at different retinal locations, when they are exposed to a transient or a steady adapting field, by comparing the sensitivity loss produced at the fovea and





**Figure 7.** Steady and transient (measured from threshold luminance at SOAO) disability glare effect for the three subjects at fovea, 6° and 9°.

peripheral retina. Calculations have been performed from data shown in Figure 6 and are depicted in Figure 7a–c.

In this figure, differences between the log luminance thresholds at zero SOA and steady light adaptation conditions, relative to the absolute log luminance threshold ( $L_t^a$ ), have been calculated for the three observers at fovea, 6° and 9° eccentricity. In the literature, these magnitudes are sometimes referred to as *transient disability glare*, ( $\log(L_t^{SOA0}/L_t^a)$ ), and *steady disability glare* ( $\log(L_t^{LA}/L_t^a)$ ). Note that these terms are usually employed when the adapting beam does not overlap the probe beam (indirect adapting beam). However, as suggested by Boynton et al.,<sup>19</sup> the effect of the onset of a direct adapting field (such as that employed in this experiment) on the temporal evolution of the sensitivity loss, is the same as that produced by an indirect adapting field of a fixed luminance.

As shown in Figure 7, transient disability glare is always greater than steady disability glare at the fovea and in the retinal periphery.<sup>4,5</sup> Furthermore, both effects increase with eccentricity, much more clearly between the fovea and 6° eccentricity. However, when comparing foveal with peripheral results, it is important to consider that a non-negligible part of the observed increase in transient and steady disability glares is due to the lowering of the absolute threshold observed in 6° eccentricity relative to that measured foveally (see Figure 3) due to rod contributions. When comparing behaviour at 6° and 9°, the observed increase in transient and steady disability glare is much lower and, mostly, due to changes in  $L_t^{SOA300}$  and  $L_t^{LA}$ .

These results confirm those obtained by Bichao et al.<sup>14</sup> in their work and extend them further in the peripheral field. In the experiment performed by Bichao et al., they employed an indirect adapting field and compared foveal and peripheral behaviour where peripheral measurements were restricted to an eccentricity of 2.8°. Our results are, however, more definitive, because they were obtained by comparing foveal and retinal periphery under the same experimental conditions rather than with different exposure times at the fovea and 2.8° eccentricity.

### Discussion

Our results regarding the speed of adaptation are consistent with the findings of Bodmann et al.<sup>13</sup> They found that, after a sensitivity loss caused by a sudden change of adaptation from 2000 to 8 cd m<sup>-2</sup>, sensitivity recovery is achieved in 500 ms, but only in areas of the retina located between 5° and 20°, while recovery is not yet complete at the foveal area by 900 ms. The slower recovery time found in our experiment, compared to that of Bodmann et al.,<sup>13,25–28</sup> may be due to the fact that, while in our

case subjects adapt to a higher light level than in the initial condition, in their experiment subjects were adapted to a lower light level than the original condition. It is well known that dark adaptation is slower than light adaptation. However, our results seem to contradict those of Bichao *et al.*<sup>14</sup> (see *Figure 5*) who reported that adaptation was reached faster at the fovea than at an eccentricity of 2.8°. The difference between these results is likely because the foveal and peripheral conditions were measured with different presentation times in their experiment. Moreover, their experiment was performed under a glare source of 140 cd m<sup>-2</sup> and the authors measured the threshold with a transient adaptation field with an SOA of 500 ms. The recovery of foveal sensitivity found by them is lower than those determined in our experiment and, therefore, the relationship between transient and steady conditions is reduced.

Other literature that supports our findings are studies which determined the critical fusion frequency of a flickering stimulus, validating the Ferry-Porter law for different areas of the retina.<sup>29,30</sup> In these studies, an increase in the slope of the critical fusion frequency vs retinal illumination was found with increasing eccentricity from the fovea up to 10° and then this slope was maintained up to eccentricities as large as 85°. This increase in speed has been hypothesized to relate to the change in cone photoreceptor outer-segment length that occurs in the periphery.<sup>31</sup> These findings were obtained in measurements where cones were isolated and, therefore, can be compared only partially with our results. The growth of the slope of the critical fusion frequency as a function of retinal illumination tells us about the increased speed of adaptation of cones that occurred in the same retinal location where we found a higher rate of sensitivity recovery. The results of Tyler and Hammer<sup>29,30</sup> also show that, in an area between 10° and 35°, that speed increment would have to reach a stability, which is consistent with findings in subjects IA and CR and might be the trend in BM for eccentricities greater than those measured (see *Figure 5*). However, we additionally found a decrease in the rate of adaptation in the area of the retina between 9° and 15° before reaching a constant value, a result not predicted by those studies.

The sensitivity of the retina at a given mesopic adaptation level is not only the result of the size and density of rods and cones in the area concerned, but also depends on the interaction between them. Lange *et al.*<sup>32</sup> investigated the influence of rod light and dark adaptation on cone-mediated sensitivity to monocular displays modulated in both spatial and temporal domains. They found that rod light adaptation increased sensitivity in the case of high spatial frequencies gratings flickering slowly and for low spatial frequencies gratings flickering rapidly.

Those effects were referred to as grating suppressive rod-cone interaction and flicker suppressive rod-cone interaction, respectively. The magnitudes of both types of rod-cone interactions increased as the retinal position of the test display was increasingly displaced parafoveally. Moreover, in parafoveal retina, both forms of suppressive rod-cone interaction increased as the overall dimension of the test stimulus decreased. Since in our experiments we have 0.45° stimulus size and a short presentation time (40 ms), a flicker suppressive rod-cone interaction could be the mechanism acting to decrease the speed of adaptation in that region of the parafovea. More recently, Zele *et al.*<sup>12</sup> showed that the lateral suppressive rod-cone interactions on flicker detection by cones produced not only a decrease in temporal contrast sensitivity but, also, a delay in cone response. This experiment was performed at 7.5° eccentricity. In order to explain the pattern of results shown in *Figure 5*, it would be necessary to combine two opposite mechanisms: on the one hand, the natural trend of peripheral cones to be faster than foveal ones; on the other, an increasing effect of rod suppression on cone delays with eccentricity. This might result in an increased speed of adaptation as we move from fovea up to 6°–9° deg eccentricity and a decrease in this variable for further eccentricities as rod-cone interaction becomes the dominant effect.

Pokorny *et al.*<sup>23</sup> measured the time course of adaptation for chromatic stimuli by using detection and hue discrimination tasks and found thresholds rise abruptly at adaptation field onset, consistent with the mediation of the parvocellular pathway. They also employed a measurement protocol and a task to constrain the thresholds to the inferred magnocellular pathway and found typical backward masking. This is also the post-receptoral pathway most strongly affected by rod-cone interaction in flicker detection as was recently showed by Cao *et al.*<sup>33</sup> in experimental conditions that control the adaptation levels of rod and cones at the same chromaticity and rod excitation level. The experiment was performed at 7.5° eccentricity. Our data seem to have the signature of the magnocellular pathway, both in fovea and in the mid-peripheral retina for all the subjects.

The lighting conditions considered in this work correspond to those in which a probe and an adaptation field overlap in some region of the retina. These can be related to two typical situations which appear in a night driving task. The first one would be the appearance of a high mesopic lighting level<sup>22</sup> onto a steady visual field whose luminance corresponds to a scotopic or low mesopic range (0.01–0.5 cd m<sup>-2</sup>). An example of this situation is the appearance of an obstacle, a pedestrian or a traffic signal in the visual field of a driver at night. The second one comes from considering as a conditioning field the



veiling luminance due to the intraocular light scatter produced by the headlights of oncoming traffic. As an example, an oncoming car placed at 20 m from us with its headlights turned on may produce a retinal illuminance of about 15 lux which is approximately equivalent to a veiling luminance of  $5 \text{ cd m}^{-2}$ .<sup>34</sup>

The results shown in this work inform us that there is an important part of the peripheral retina (in the range from  $3^\circ$  to  $9^\circ$ ) which is able to adapt faster than the fovea. However, it should also be considered that adaptation in that retinal area does not produce such an important recovery as that produced at the fovea. As shown in Figure 6, all observers have a sensitivity which is at least 0.5 log units greater in the fovea than in the retinal periphery at steady adaptation conditions. Even for transient adaptation fields the fovea shows greater sensitivity than the retinal periphery. From a practical point of view, one could think that, even under mesopic lighting conditions, the fovea is the part of the retina that provides the best information to the visual system in order to make decisions which may be critical for tasks such as night driving. However, all we know is that peripheral vision plays an undeniable role, that of detecting stimuli out of the central field of view. This detection leads the brain to foveate those stimuli later in order to identify them.

It is true that the phenomena analyzed in our work is concerned with early adaptation processes operating at the fovea and periphery responding to rapid changes in lighting conditions. In this sense, our results for the speed of adaptation are different from those obtained by Plainis et al.<sup>15</sup> although we can also conclude, as they did, that this relates to greater sensitivity in the fovea than that in the periphery.

Another important conclusion arises from the results obtained in this work. Data obtained in fovea showed behaviour mostly due to cone function. This might lead us to conclude that, when the conditioning field is around  $5 \text{ cd m}^{-2}$ , the adaptation process corresponds to a photopic behaviour. However, the results found for the retinal periphery, particularly from  $6^\circ$  and more, showed that rods may play a non-negligible role in the adaptation process, as would be expected for the mesopic range, at least in terms of the speed of adaptation. These results might propose a new scenario in the concept of limits of the photopic and mesopic ranges of illumination. In this new scenario, in order to establish these limits, perhaps it would be convenient to specify not only the luminance level, the spectral distribution of the illuminant, and the spatio-temporal properties of the stimulus, but also the retinal area involved as well as the analyzed visual function.

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