



**Repositorio Institucional de la Universidad Autónoma de Madrid**

<https://repositorio.uam.es>

Esta es la **versión de autor** del artículo publicado en:  
This is an **author produced version** of a paper published in:

Brain Topography 29.6 (2016): 847–855

**DOI:** <http://dx.doi.org/10.1007/s10548-016-0510-6>

**Copyright:** © Springer Science+Business Media New York 2016

El acceso a la versión del editor puede requerir la suscripción del recurso  
Access to the published version may require subscription

## **Ambient light modulation of exogenous attention to threat**

Luis Carretié<sup>1,\*</sup> and Elisabeth Ruiz-Padial<sup>2</sup>

<sup>1</sup> Luis Carretié, Facultad de Psicología, Universidad Autónoma de Madrid, 28049 Madrid,  
Spain

<sup>2</sup> Elisabeth Ruiz-Padial, Departamento de Psicología, Universidad de Jaén, 23071 Jaén,  
Spain

\* Corresponding autor: carretie@uam.es

### **Acknowledgements**

This research was supported by the grants PSI2014-54853-P and PSI2012-37090 from the *Ministerio de Economía y Competitividad* of Spain (MINECO).

## **Abstract**

Planet Earth's motion yields a 50% day - 50% night yearly balance in every latitude or longitude, so survival must be guaranteed in very different light conditions in many species, including human. Cone- and rod-dominant vision, respectively specialized in light and darkness, present several processing differences, which are—at least partially—reflected in event-related potentials (ERPs). The present experiment aimed at characterizing exogenous attention to threatening (spiders) and neutral (wheels) distractors in two environmental light conditions, low mesopic (L, 0.03 lux) and high mesopic (H, 6.5 lux), yielding a differential photoreceptor activity balance: rod>cone and rod<cone, respectively. These distractors were presented in the lower visual hemifield while the 40 participants were involved in a digit categorization task. Stimuli, both targets (digits) and distractors, were exactly the same in L and H. Both ERPs and behavioral performance in the task were recorded. Enhanced attentional capture by salient distractors was observed regardless of ambient light level. However, ERPs showed a differential pattern as a function of ambient light. Thus, significantly enhanced amplitude to salient distractors was observed in posterior P1 and early anterior P2 (P2a) only during the H context, in late P2a during the L context, and in occipital P3 during both H and L contexts. In other words, while exogenous attention to threat was equally efficient in light and darkness, cone-dominant exogenous attention was faster than rod-dominant, in line with previous data indicating slower processing times for rod- than for cone-dominant vision.

**Keywords:** Exogenous attention, ambient light, threat, event-related potentials, photoreceptors.

## Introduction

Planet Earth's rotation, translation and precession dynamics yield a yearly equivalent time for day and night in every latitude and longitude of the globe. This means that survival must be guaranteed both in light and darkness in the majority of species, including humans. In order to cover the full range of environmental light intensities ( $10^{10}$ ; Sterling 2003), different visual mechanisms have evolved for dark and light situations. In the case of humans and other vertebrates, the visual system comes with two types of retinal photoreceptors. Rods (which are  $\approx 95\%$  of photoreceptors; Jonas et al. 1992), are specialized in visual processing during darkness. Cones, the second type, are involved in daylight, or artificially equivalent situations.

Both types of photoreceptors diverge in the way they process our environment, and transmit differential information, due to their molecular bases and their retinal distribution (Curcio et al. 1990; Kawamura and Tachibanaki 2008). Rods are absent in the fovea, and the rod-cone anatomical ratio ranges from 1:1 at 0.4 mm eccentricity from central fovea to approximately 30:1 at 10 mm eccentricity. It is important to note that this differentiation at the photoreceptor level is also reflected in subsequent visual architecture. Thus, the visual route from retina to striate cortex consists of two parallel streams, the magnocellular and the parvocellular pathways. They originate from different retinal ganglion cells (Perry et al. 1984), which project to separate layers of the lateral geniculate nucleus (LGN) of the thalamus (Livingstone and Hubel 1987). Critically, although rod and cone outputs join at the retinal ganglion cell level (Masland 2001; Wässle 2004), rod signals have been reported to be preferentially (but not exclusively) conveyed through the magnocellular pathway in primates (Benedek et al. 2003; Lee et al. 1997).

An unexplored question that arises is how this physiological differentiation influences the efficiency with which we process the environment in very dark and light

situations, particularly—considering their potentially dramatic effects on survival—those stimuli associated with threat or danger. The present study explored this issue, focusing more specifically on how exogenous attention to emotional stimuli is modulated by environmental light conditions. Exogenous attention, also termed automatic or bottom-up attention, among other terms, can be understood as an adaptive tool that permits the detection and processing of salient events that appear out of the current focus of attention.

The modulatory effect of ambient light on the neural indices of exogenous attention was explored via event-related potentials (ERPs). This temporally agile neural signal is of special interest for two reasons. First, certain ERP components are reliable indices of exogenous attention, such as the posterior P1 (P1p) or the anterior P2 (P2a), both showing enhanced amplitude in response to stimuli capturing exogenous attention (see a review in Carretié 2014). Second, visual ERPs have shown sensitivity, from  $\approx 100$  to  $\approx 400$  ms (this includes P1p and P2a), to photoreceptor activity (Cohn and Hurley 1985; Parisi et al. 2010; Rudvin and Valberg 2006), to parvo- vs. magnocellular activity (Elleberg et al. 2001; Hammarrenger et al. 2007) and, importantly, to the ambient light modulation of visual perception of discrete (non-emotional) visual stimuli (Münch et al. 2014).

Two ambient light conditions were designed in this experiment, one close to the low mesopic threshold ( $\approx 0.03$  lux) and the other close to the high mesopic threshold ( $\approx 6.5$  lux). Mesopic vision is a wide intermediate stage between pure rod or scotopic vision and pure cone or photopic vision (Narisada and Schreuder 2004; Stockman and Sharpe 2006; Zele and Cao 2014). It, approximately, ranges from starlight to twilight (Stockman and Sharpe 2006), and is present in many indoor environments, including the majority of Human Neuroscience laboratories. From the low threshold of mesopic vision (i.e. that shared with scotopic) to the high threshold (shared with photopic vision), there is a gradual change in the rod/cone functional bias, from 100%/0% contribution to visual processing to

0%/100% (Schreuder 2008). Thus, although both rods and cones were active in both conditions of our experiment, their balance varied. Our main hypothesis, based on evolutionary considerations, is that threatening distractors will also efficiently capture exogenous attention in the very dark (low mesopic / rod dominant) ambient light situation. However, and taking into account previous ERP data mentioned above, we expect differences at the neural level between rod- and cone-originated exogenous attention in the 100 to 400 ms latency. Due to the lack of previous information on this particular issue, no specific predictions can be formulated on particular ERP components reflecting these differences or on whether they will be produced in the temporal or in the amplitude domain (or in both).

## **Material and Methods**

### **Participants**

This study had been approved by the Research Ethics Committee of the Universidad de Jaén. Forty-two individuals participated in this experiment, although data from only 40 of them could eventually be analyzed, as explained later (28 women, age range of 17 to 31 years, mean=19.32, SD=3.24). All participants were students of Psychology at the Universidad de Jaén and took part in the experiment voluntarily after providing informed consent. They reported normal or corrected-to-normal visual acuity.

### **Stimuli and procedure**

Participants were placed in an electrically shielded, sound-attenuated room, and stimuli were presented on a CRT screen (16 inches, 85 Hz). Their face distance from the screen was 60 cm. Stimuli are illustrated in Figure 1, in which luminosities of several elements have been increased to make them easier to view (a figure showing original luminosities as presented in the experiment is available at [www.uam.es/CEACO/sup/LuzAmb15.htm](http://www.uam.es/CEACO/sup/LuzAmb15.htm)).

Stimuli consisted of a black background (0, 0, 0 in the RGB scale, ranging from 0 to 255 in red, green and blue, respectively; 255, 255, 255 would indicate absolute white), and four non-black elements: a fixation diamond and two digits located left and right from fixation, all in dark blue (0, 0, 34), and a dark gray distractor (17, 17, 17) below fixation. Distance from the inner border to the center of the fixation diamond ( $1.05^\circ \times 1.05^\circ$  visual angle size) was  $1.8^\circ$  in the case of digits, and  $5.5^\circ$  in the case of distractors. Distractors were of two types: threatening (T), which consisted of spiders, and neutral (N), which consisted of wheels. Spiders and wheels covered an approximate area of  $10.5^\circ \times 10.5^\circ$ , shared a similar figure (against ground) surface and had similar spatial frequencies (see [www.uam.es/CEACO/sup/LuzAmb15.htm](http://www.uam.es/CEACO/sup/LuzAmb15.htm) for details).

The task was related to the two digits ( $1.4^\circ \times 2.2^\circ$ ): participants were required to press, “as accurately and rapidly as possible”, one key if both digits were even or if both were odd (i.e. if they were “concordant”), and a different key if one digit was even and the other was odd (i.e. if they were “discordant”). There were 32 combinations of digits, half of them were concordant and the other half discordant. The same combination of digits was repeated in T and N trials, in order to ensure that task demands were the same in the two distractor conditions. Subjects were instructed to maintain their gaze towards the fixation diamond, which never disappeared, and to avoid blinking as much as possible.

Each stimulus was presented for 200 ms, and inter-trial interval (ITI) was random between 2200 ms and 3000 ms (average ITI was 2600 ms). Thirty-two trials for each of the two distractor conditions (T and N) were presented, yielding a total of 64 trials. The order of trials was randomized. An eight-trial practice block, without distractors, was previously presented to each participant.

\*\*\* Figure 1 about here \*\*\*

The Psychophysiology Laboratory at the Universidad de Jaén, in which this experiment was run, has double-door access and no windows, so it allows for complete darkness. Recording sessions were all performed during daylight time. In the darker environment block (low mesopic, “L”), all lights were turned off with the exception of the screen with the task, so illuminance was  $\approx 0.03$  lux (as measured in pilot studies by an *Iso-Tech ILM 1337 light meter* placed in front of subject’ eyes and facing the light sensor towards the CRT screen while presenting a stimulus). In the lighter environment block (high mesopic, “H”), the adjustable light in the laboratory was set so illuminance measured in subjects’ eyes was  $\approx 6.5$  lux (measured in the same conditions). The same 64-trial run explained above was presented twice to subjects, one in the L block and the other in the H block, yielding 4 conditions: TL, NL, TH, and NH. L and H environments were counterbalanced: 20 out of the 40 participants began with L, and the rest with H. Before each block, participants were asked to wait for a 10 minute adaptation period to light conditions. This task followed, both in L and H, a three and a half minute independent and unrelated task consisting of the passive viewing of a sequence of dark squares (17, 17, 17 in the RGB scale) presented at different locations on a black background (0, 0, 0); this unrelated task aimed at characterizing perceptual processing in both light environments (see details in Carretié et al. 2015).

### **Recording and pre-processing**

Electroencephalographic (EEG) activity was recorded using *BrainVision system* (Brain Products, Munich, Germany) with an electrode cap (*ElectroCap International*) with tin electrodes. Twenty-eight electrodes were placed on the scalp following a homogeneous distribution. All scalp electrodes were referenced to the nosetip. Electrooculographic (EOG) data were recorded supra- and infraorbitally (vertical EOG) as well as from the left versus right orbital rim (horizontal EOG). An online analog bandpass filter of 0.3 Hz to 40



Hz was applied. Recordings were continuously digitized at a sampling rate of 500 Hz. The continuous recording was divided into 700 ms epochs for each trial, beginning 100 ms before stimulus onset.

Ocular artifact removal was carried out through an independent component analysis (ICA)-based strategy (Jung et al. 2000), as provided in the *BrainVision Analyzer* software (Brain Products, Munich, Germany). After the ICA-based removal process, a second stage of visual inspection of the EEG data was conducted. If any further artifact was present, the corresponding trial was discarded. Additionally, trials in which the participant responded erroneously, or did not respond, were eliminated from analyses. This incorrect response and artifact rejection procedure led to the average admission of 26.53 (SD=3.49) trials in the TH condition, 27.08 (2.75) in NH, 26.58 (3.37) in TL, and 26.98 (3.08) in NL, with 19 being the minimum number of accepted trials in any condition. Data from one participant was discarded due to non-solvable anomalies in the recordings of more than 10% leads, and another participant was aleatorily discarded to reach a complete L/H counterbalance and to ensure the same male/female proportion (6/14) in both groups (i.e., L first and H first).

### **Data analysis**

Prior to statistical contrasts on amplitudes, an off-line bandpass filter of 1.5 Hz to 15 Hz was applied; this filter guaranteed that relevant frequencies, revealed as critical to study ERP responses to visual stimuli in the same ambient lightings, passed the filter (Carretié et al., 2015), and minimized the effect of spurious, noisy amplitude and latency differences among conditions. The windows of interest (WOI; i.e., the ERP temporal interval within which amplitudes were quantified) for each component were established based on visual inspection of grand averages. Repeated-measure ANOVAs involving three factors,

Distractor (two levels: T and N), Light (two levels: L and H), and Electrode (number of levels were defined for each relevant component after visual inspection of grand averages), were carried out on component peak amplitudes, and, if grand averages suggested temporal differences, also on component latencies. Effect sizes were computed using the partial eta-square ( $\eta^2_p$ ) method. Post-hoc comparisons to determine the significance of pairwise contrasts were performed using the Bonferroni correction procedure ( $\alpha=0.05$ ).

Additionally, behavioral performance in the digit categorization task was analyzed through two parameters: reaction times (RTs) and accuracy. Since these parameters rarely fit to a normal distribution, non-parametric tests (Wilcoxon signed-rank procedure) were employed to test the effects of Distractor and Light on RTs and accuracy.

## Results

As shown in Figure 2, visual inspection of grand averages suggested that P1p, P2a and occipital P3 (P3o) were the most sensitive components to the experimental manipulation<sup>1</sup>. Table 1 shows the mean and the standard error of means of their amplitudes as well as the main results of the three-way ANOVAs (see Methods section). Levels of factor Electrode were variable for each component and included electrode sites where P1p, P2a and P3o were prominent both in the present and in previous studies (Hopfinger & Mangun, 2001, Carretié et al. 2013b; Luck 2012). As a result, Electrode levels were three (O1, Oz, O2), six (F3, Fz, F4, FC3, FCz, and FC4) and three (O1, Oz, O2) for P1p, P2a and P3o, respectively. A result common to P1p, P2a and P3o was that factor Electrode did not significantly interact with either Distractor or with Light nor with their interaction, an index of optimal electrode configuration of each of the three scalp regions in terms of their

---

<sup>1</sup> The conspicuous N2 at occipital sites was also analyzed despite the lack of an effect of Distractor in grand averages (and hence falling outside the scope of this study). Effects were non-significant:  $F(1,39)<1$  and  $p>0.4$  in all relevant contrasts: Light, Distractor, LightxDistractor, Electrodes(O1, Oz, O2)xLightxDistractor.

functional homogeneity (for brevity, we do not describe these results on Electrode here, but they are available at <http://www.uam.es/CEACO/sup/LuzAmb15.htm>).

\*\*\* Table 1 and Figure 2 about here \*\*\*

### **P1p**

A WOI between 120 and 150 ms was defined to quantify P1p peak amplitude (see the Methods section). Amplitudes were quantified in recordings obtained at occipital locations (O1, Oz and O2), where the P1p was prominent (see Figure 2). Therefore, a 2x2x3 (Distractor x Light x Electrode) ANOVA was carried out (see details in Methods section). An interaction Distractor x Light was revealed by ANOVAs ( $F(1,39)=4.245$ ,  $p=0.043$ ,  $\eta^2_p=0.098$ ). Bonferroni post-hoc tests indicated that amplitudes were significantly greater in response to T distractors, as compared to N distractors, in the H lighting condition ( $p=0.033$ ). No main effects of Light or Distractor were observed (Table 1).

### **P2a**

In this case, as illustrated in Figure 2, a conspicuous latency effect was apparent in grand averages. Consequently, a wide WOI between 170 and 260 ms was defined to quantify both the peak amplitude and latency of P2a. The electrodes in which these parameters were quantified for each subject and condition were those placed on fronto-central locations (F3, Fz, F4, FC3, FCz, and FC4), where the P2a was prominent (see Figure 2). Thus, two 2x2x6 (Distractor x Light x Electrode) ANOVA were computed, one on latencies and the other on amplitudes (see Methods section).

On the one hand, a significant main effect of Light was observed on P2a *latency* ( $F(1,39)=9.341$ ,  $p=0.004$ ,  $\eta^2_p=0.193$ ). As also observed in Figure 2, latencies were longer

for L than for H environments. The effects of Distractor and of the Distractor x Light interaction on latency were not significant (Table 1). On the other hand, with respect to P2a peak *amplitude*, ANOVAs showed a significant main effect of Distractor ( $F(1,39)=4.604$ ,  $p=0.038$ ,  $\eta^2_p=0.106$ ). Concretely, and as illustrated in Figure 2, amplitudes were greater in response to T than to N. In other words, both the early P2a (sensitive to H environments, according to previous latency analyses) and the late P2a (sensitive to L) presented maximal amplitude in response to T distractors. No significant effects of Light nor Distractor x Light interaction were observed (Table 1).

### **P3o**

A WOI between 260 and 320 ms was defined to measure P3o amplitude. This parameter was quantified in recordings obtained at occipital locations (O1, Oz and O2), where P3o presented maximal amplitudes (see Figure 2). Distractor x Light x Electrode (2x2x3) ANOVAs showed a significant main effect of Distractor ( $F(1,39)=5.026$ ,  $p<0.05$ ,  $\eta^2_p=0.114$ ). Concretely, and as illustrated in Figure 2, amplitudes were greater in response to T than to N. Neither the effects of Light nor those of the Distractor x Light interaction reached significance (Table 1).

### **Behavior**

Table 2 shows the mean and the standard error of means of accuracy and RTs (see Methods section). Non-parametric Wilcoxon tests (see Methods section) on behavior performance in the digit categorization task showed a trend with respect to the effect of Distractor on accuracy ( $Z=-1.829$ ,  $p=0.067$ ), T stimuli being associated with more errors than N. Effects of Light on accuracy, as well as effects of both Distractor and Light on RTs were not significant ( $p>0.1$  in all cases).

\*\*\* Table 2 about here \*\*\*

## Discussion

This study explored the modulatory effect of ambient light (low mesopic vs. high mesopic) on exogenous attention to threatening and neutral distractors. Two conclusions may be extracted from the observed results. First, both low and high mesopic contexts were associated with neural and behavioral indices of enhanced exogenous attention to threatening distractors. Neural indices consisted of enhanced amplitudes in response to spiders in three components: P1p, P2a and P3o. Behavioral indices consisted of a statistical trend pointing to more errors in the ongoing digit categorization task in spider trials. Second, neural effects were modulated by the ambient light. Thus, P1p and early P2a were only sensitive to the emotional content of distractors in the high mesopic context, late P2a only in the low mesopic context, and P3o in both light contexts. These conclusions will be developed next.

**On P1p, P2a and P3o sensitivity to threatening distractors.** Sensitivity to threatening distractors of these three components was observed in at least one ambient light condition (this factor will be discussed later). Enhanced amplitudes of P1p (or posterior P1) in response to spiders presented as distractors in tasks similar to that employed here (concurrent but distinct target-distractor tasks, or CDTD) have previously been reported (Carretié et al 2005; Carretié et al. 2009). Additionally, sensitivity of P2a (or anterior P2) to the emotional content of distractors has been frequently reported too, with greater amplitudes for negative distractors, as compared to neutral, being consistently found (Carretié et al. 2004; 2005; 2011; 2013b; Feng et al. 2012; Holmes et al. 2006; Junhong et al. 2013). Finally, P3o (or occipital P3, since it showed maximal amplitudes in this scalp region) has been also reported in CDTD tasks, such as visual search tasks (Luck 2012), and must be distinguished from the well-known centro-parietal P3 or P3b, and from fronto-central P3, also termed P3a or novelty P3. While the effects of emotionally negative

non-target stimuli on P3a and P3b have been previously explored (Delplanque et al. 2005; Feng et al. 2012; Kim et al., 2013; Stanford et al. 2001), data about P3o are very scarce, as well as proposals on its functional meaning. Moreover, it has not been described in previous studies employing *emotional* CDTD tasks. Whereas it has been associated with response to targets (Luck 1994), the present study, in which targets were exactly the same in threatening and neutral distractor trials, suggests a significant influence of distractors, at least when they present threatening value.

**On P1p and P2a modulation by ambient light.** As indicated, P1p and early P2a showed maximal sensitivity to threatening distractors in high mesopic contexts, while late P2a did so in low mesopic contexts (the present study did not find any difference in P3o as a function of ambient light). Therefore, results suggest that, although both rod- and cone-dominant vision guarantee the detection of threat, their latencies differ. The fact that low mesopic and high mesopic vision modulate ERPs recorded in response to discrete visual stimuli in the temporal domain rather than in the amplitude domain has been recently reported (Carretié et al. 2015). Present results are consistent with the fact that speed of processing is greater in the case of cones than in the case of rods, which has been well known for nearly a century (Ives 1922), and has been repeatedly confirmed (Kilavik and Kremers 2001; MacLeod 1972; Sharpe et al. 1989).

In general, current results are in line with previous studies showing visual ERP components sensitivity to specific photoreceptor action. P1p has been associated with cone activity in previous ERP studies employing different tasks (Parisi et al. 2010; Rudvin and Valberg 2006; but see Cohn and Hurley 1985). Posterior P2 has been also reported to be sensitive to photoreceptor activity (Cohn and Hurley 1985; Rudvin and Valberg 2006). P2a has not been previously explored in this respect, but present results suggest that the early

P2a is mainly associated with cone-originated neural activity and the late P2a with rod-originated activity.

**Beyond photoreceptors.** As mentioned in the Introduction, rod signals have been reported to be preferentially, but not exclusively, conveyed by the magnocellular pathway in primates (Benedek et al. 2003; Lee et al. 1997; Purpura et al. 1988; Sun et al. 2001), while neither a clear parvo- nor magnocellular bias has been reported for cone signals. In other terms, the magnocellular (but not the parvocellular) visual processing system presents a balanced activity in both light and darkness, so it seems crucial in guaranteeing efficient exogenous attention to threat in every light level. In relation to this, a key role of the magnocellular visual system (despite the fact it conveys poorer information than parvocellular in terms of form details or color) in exogenous attention has previously been proposed (Laycock and Crewther 2008). Indeed, in studies in which some parameters that are differentially processed by the magnocellular and the parvocellular systems are manipulated, such as eccentricity, spatial frequency or motion, “magnocellular characteristics” tend to better capture exogenous attention (e.g., Carretié, Albert et al. 2013a; Franconeri and Simons 2003; 2005; Vuilleumier et al. 2003).

A question that arises is how compatible photoreceptor-related results are with magnocellular and parvocellular response latencies. Concretely, the fact that P1p and early P2a reflect cone-dominant vision and that rod-dominant is reflected later, in late P2a and P3o, seems in conflict with the extended idea that the magnocellular (rod biased) system is faster than the parvocellular. This issue is of maximal interest to be explored in future studies, however, two relevant comments are worth mentioning at this point. On one hand, the detection of the first significant effects in P1p does not necessarily mean that there are no other previous effects to which ERPs are insensitive (EEG is blind to part of brain activity due to the electrical structure of the brain: Nunez and Srinivasan, 2006). On the

other hand, and importantly, the magnocellular latency advantage over parvocellular latency is lost at the neocortical level, as revealed by intracranial recordings in primates (Maunsell et al., 1999).

**Conclusions and future directions.** In sum, present results support the hypothesis, motivated by evolutionary considerations, that both rod- and cone-dominant vision, despite their important physiological differences, equally guarantee an efficient detection of threat. However, each of these types of vision leaves a different neural trace, manifested in the temporal domain: cone-biased exogenous attention is preferentially reflected in P1p and early P2a, while rod-biased exogenous attention is preferentially reflected in late P2a. Occipital P3, or P3o, which was also sensitive to threatening distractors, was equally influenced by rod- and cone-dominant vision. Due to their high temporal resolution, ERPs are a particularly useful tool to explore the influence of environmental light in exogenous attention.

Four final considerations of methodological and theoretical nature are worth taking into account in future studies. First, ambient light is an important factor to control in studies exploring exogenous attention, since, as shown here, it strongly modulates latencies and amplitudes of components such as P1p and P2a. Second, the observed effects were produced within mesopic vision (low or rod-biased and high or cone-biased). It may be expected that the effects are reinforced in more extreme conditions, such as comparing scotopic vs. photopic vision (i.e., pure rod vs. pure cone vision). Whereas these extreme conditions are technically difficult to implement, future steps should try to introduce them, in order to advance this unexplored field. Third, future research on this topic would benefit from increasing signal-to-noise ratio by introducing more trials for each condition. In particular, present results on P1p, showing the lowest amplitude among those components reflecting sensitivity to the experimental manipulations, need confirmation in future studies



employing an increased number of trials. Finally, in the theoretical plane, exploring whether the observed effects are circumscribed to threat specifically or may be explained by wider factors, such as cognitive/affective meaning or saliency of stimuli, would be of maximal interest, and could be investigated by introducing other non-threatening salient conditions.

## References

- Benedek, G, Benedek, K, Kéri, S, Letoha, T, Janáky, M (2003) Human scotopic spatiotemporal sensitivity: A comparison of psychophysical and electrophysiological data. *Doc. Ophthalmol.* 106, 201–207.
- Carretié L (2014) Exogenous (automatic) attention to emotional stimuli: A review. *Cogn. Affect. Behav. Neurosci.* 14, 1228–1258.
- Carretié L, Albert J, López-Martín S, Hoyos S, Kessel D, Tapia M, Capilla A (2013a) Differential neural mechanisms underlying exogenous attention to peripheral and central distracters. *Neuropsychologia* 51, 1838–1847.
- Carretié L, Hinojosa JA, López-Martín S, Albert, J, Tapia M, Pozo MA (2009) Danger is worse when it moves: Neural and behavioral indices of enhanced attentional capture by dynamic threatening stimuli. *Neuropsychologia* 47, 364–369.
- Carretié L, Hinojosa JA, Martín-Loeches M, Mercado F, Tapia M (2004) Automatic attention to emotional stimuli: Neural correlates. *Hum. Brain Mapp.* 22, 290–299.
- Carretié L, Hinojosa JA, Mercado F, Tapia M (2005) Cortical response to subjectively unconscious danger. *Neuroimage* 24, 615–623.
- Carretié L, Kessel D, Carboni A, López-Martín S, Albert J, Tapia M, Mercado F, Capilla A, Hinojosa JA (2013b) Exogenous attention to facial vs non-facial emotional visual stimuli. *Soc. Cogn. Affect. Neurosci.* 764–773.

- Carretié L, Ruiz-Padial E, López-Martín S, Albert J (2011) Decomposing unpleasantness: Differential exogenous attention to disgusting and fearful stimuli. *Biol. Psychol.* 86, 247–253.
- Carretié L, Ruiz-Padial E, Mendoza MT (2015) An event-related potential study on the interaction between lighting level and stimulus spatial location. *Front. Hum. Neurosci.* 9, 637.
- Cohn R, Hurley CW (1985) Differential visual evoked cortical responses to direct and peripheral stimulation in man. *Electroencephalogr. Clin. Neurophysiol.* 61, 157–160.
- Curcio CA, Sloan KR, Kalina RE, Hendrickson AE (1990) Human photoreceptor topography. *J. Comp. Neurol.* 292, 497–523.
- Delplanque S, Silvert L, Hot P, Sequeira H (2005) Event-related P3a and P3b in response to unpredictable emotional stimuli. *Biol. Psychol.* 68, 107–120.
- Ellemberg D, Hammarrenger B, Lepore F, Roy M, Guillemot J (2001) Contrast dependency of VEPs as a function of spatial frequency: The parvocellular and magnocellular contributions to human VEPs. *Spatial Vision* 15, 99–111.
- Feng C, Wang L, Wang N, Gu R, Luo Y (2012) The time course of implicit processing of erotic pictures: An event-related potential study. *Brain Res.* 1489, 48–55.
- Franconeri SL, Simons DJ (2003) Moving and looming stimuli capture attention. *Percept. Psychophys.* 65, 999–1010.
- Franconeri SL, Simons DJ (2005) The dynamic events that capture visual attention: A reply to abrams and christ (2005) *Percept. Psychophys.* 67, 962–966.
- Hammarrenger B, Roy M, Ellemberg D, Labrosse M, Orquin J, Lippe S, Lepore F (2007) Developmental delay and magnocellular visual pathway function in very-low-birthweight preterm infants. *Dev. Med. Child Neurol.* 49, 28–33.

- Holmes A, Kiss M, Eimer M (2006) Attention modulates the processing of emotional expression triggered by foveal faces. *Neurosci. Lett.* 394, 48–52.
- Hopfinger JB, Mangun GR (2001) Electrophysiological studies of reflexive attention. In: Folk CL, Gibson BS (Eds.), *Attraction, distraction and action: Multiple perspectives on attentional capture*, Elsevier, New York, NY, pp. 3–26.
- Ives HE. (1922) Critical frequency relations in scotopic vision. *J. Opt. Soc. Am.* 6, 254–267.
- Jonas JB, Schneider U, Naumann GO (1992) Count and density of human retinal photoreceptors. *Graef. Arch. Clin. Exp.* 230, 505–510.
- Jung TP, Makeig S, Humphries C, Lee TW, Mckeown MJ, Iragui, V, Sejnowski TJ (2000) Removing electroencephalographic artifacts by blind source separation. *Psychophysiology* 37, 163–178.
- Junhong H, Renlai Z, Senqi H (2013) Effects on automatic attention due to exposure to pictures of emotional faces while performing Chinese word judgment tasks. *PLoS One*, 8(10), e75386.
- Kawamura S, Tachibanaki S (2008) Rod and cone photoreceptors: Molecular basis of the difference in their physiology. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* 150, 369–377.
- Kilavik BE, Kremers J (2001) Rod and L-cone interactions in a deuteranope at different temporal frequencies. *Color Res. Appl.* 26(S1), S76–S78.
- Kim EY, Lee S, Park G, Kim S, Kim I, Chae J, Kim H T (2013) Gender difference in event related potentials to masked emotional stimuli in the oddball task. *Psych. Investig.* 10, 164–172.

- Laycock R, Crewther SG (2008) Towards an understanding of the role of the 'magnocellular advantage' in fluent reading. *Neurosci. Biobehav. R.* 32, 1494–1506.
- Lee BB, Smith VC, Pokorny J, Kremers J (1997) Rod inputs to macaque ganglion cells. *Vision Res.* 37, 2813–2828.
- Livingstone MS, Hubel DH (1987) Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. *J. Neurosci.* 7, 3416–3468.
- Luck SJ (1994) Electrophysiological correlates of feature analysis during visual search. *Psychophysiology* 31, 291–308.
- Luck SJ (2012) Electrophysiological correlates of the focusing of attention within complex visual scenes: N2pc and related electrophysiological correlates. In: Luck SJ, Kappenman ES (Eds.), *The Oxford handbook of event-related potential components*, Oxford University Press, Oxford, pp. 329–360.
- MacLeod DI (1972) Rods cancel cones in flicker. *Nature*, 235, 173–174.
- Masland RH (2001) The fundamental plan of the retina. *Nat. Neuroscience* 4, 877–886.
- Maunsell JHR, Ghose GM, Assad JA, McAdams CJ, Boudreau CE, Noerager BD (1999) Visual response latencies of magnocellular and parvocellular LGN neurons in macaque monkeys. *Vis. Neurosci.* 16, 1–14.
- Münch M, Plomp G, Thunell E, Kawasaki A, Scartezzini J, Herzog MH (2014) Different colors of light lead to different adaptation and activation as determined by high-density EEG. *NeuroImage* 101, 547–554.
- Narisada K, Schreuder D (2004) *Light pollution handbook*. New York, NY: Springer.
- Nunez PL, Srinivasan R (2006) *Electric fields of the brain: The neurophysics of EEG*. Oxford University Press, Oxford.

- Parisi V, Ziccardi L, Stifano G, Montrone L, Gallinaro G, Falsini B (2010) Impact of regional retinal responses on cortical visually evoked responses: Multifocal ERGs and VEPs in the retinitis pigmentosa model. *Clin. Neurophysiol.* 121, 380–385.
- Perry V, Oehler R, Cowey A (1984) Retinal ganglion cells that project to the dorsal lateral geniculate nucleus in the macaque monkey. *Neuroscience*, 12, 1101–1123.
- Purpura K, Kaplan E, Shapley RM (1988) Background light and the contrast gain of primate P and M retinal ganglion cells. *P. Natl. Acad. Sci. USA.* 85, 4534–4537.
- Rudvin I, Valberg A (2006) Flicker VEPs reflecting multiple rod and cone pathways. *Vision Res.* 46, 699–717.
- Schreuder D (2008) *Outdoor lighting: Physics, vision and perception*, Springer, New York.
- Sharpe LT, Stockman A, MacLeod DIA (1989) Rod flicker perception: Scotopic duality, phase lags and destructive interference. *Vision Res.* 29, 1539–1559.
- Stanford MS, Vasterling JJ, Mathias CW, Constans JI, Houston RJ (2001) Impact of threat relevance on P3 event-related potentials in combat-related post-traumatic stress disorder. *Psych. Res.* 102, 125–137.
- Sterling P (2003) How retinal circuits optimize the transfer of visual information. In: Chalupa L, Werner J (Eds.), *The visual neurosciences*, MIT Press, Cambridge, pp. 234–259.
- Stockman A, Sharpe LT (2006) Into the twilight zone: The complexities of mesopic vision and luminous efficiency. *Ophthal. Physl. Opt.* 26, 225–239.
- Sun H, Pokorny J, Smith VC (2001) Brightness induction from rods. *J. Vision* 1, 32–41.
- Vuilleumier P, Armony JL, Driver J, Dolan RJ (2003) Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nat. Neurosci.* 6, 624.

Wässle H (2004) Parallel processing in the mammalian retina. *Nat. Rev. Neurosci.* 5, 747–757.

Zele AJ, Cao D (2014) Vision under mesopic and scotopic illumination. *Front. Psychol.* 5, 1594.

**Table 1.** Means and standard error of means (SEM) of P1p, P2a and P3o amplitudes and P2a latencies to each experimental condition and three-way ANOVA results regarding Distractor and Light factors, showing significant results in bold letters (TH, threatening distractors in high mesopic vision; NH, neutral distractors in high mesopic vision; TL, threatening distractors in low mesopic vision; NL, neutral distractors in low mesopic vision). A version of this table including (non-significant) ANOVA results regarding interactions of factor Electrode with Distractor, Light and Distractor x Light is available at [www.uam.es/CEACO/sup/LuzAmb15.htm](http://www.uam.es/CEACO/sup/LuzAmb15.htm).

	Means (SEMs)				ANOVAs					
					Distractor		Light		Distractor x Light	
	TH	NH	TL	NL	F(1,39)	p	F(1,39)	p	F(1,39)	p
<b>P1p (<math>\mu</math>V)</b>	2.949 (-0.608)	1.94 (-0.561)	1.379 (-0.564)	1.719 (-0.771)	0.592	0.446	1.619	0.211	<b>4.245</b>	<b>0.046</b>
<b>P2a (<math>\mu</math>V)</b>	5.102 (-0.673)	3.958 (-0.544)	5.521 (-0.714)	4.806 (-0.81)	<b>4.604</b>	<b>0.038</b>	0.824	0.37	0.299	0.588
<b>P2a latency (ms)</b>	213.1 (-5.415)	208.775 (-5.053)	224.783 (-4.839)	226.05 (-5.094)	0.177	0.676	<b>9.341</b>	<b>0.004</b>	0.8	0.377
<b>P3o (<math>\mu</math>V)</b>	4.333 (-0.625)	3.704 (-0.568)	4.339 (-0.49)	3.578 (-0.496)	<b>5.029</b>	<b>0.031</b>	0.017	0.897	0.051	0.822

**Table 2.** Means and standard error of means (SEM) of behavioral responses (accuracy and reaction times –RTs-) to each experimental condition (TH, threatening distractors in high mesopic vision; NH, neutral distractors in high mesopic vision; TL, threatening distractors in low mesopic vision; NL, neutral distractors in low mesopic vision).

		<b>TH</b>	<b>NH</b>	<b>TL</b>	<b>NL</b>
<b>Accuracy (0 to 1)</b>	Mean	0.843	0.859	0.842	0.856
	<i>SEM</i>	<i>0.017</i>	<i>0.135</i>	<i>0.154</i>	<i>0.15</i>
<b>RTs (ms)</b>	Mean	1007.456	1005.241	1007.363	1007.524
	<i>SEM</i>	<i>25.925</i>	<i>27.387</i>	<i>29.881</i>	<i>30.643</i>



## Figure legends

**Figure 1.** Schematic representation of the stimulus sequence showing duration of stimuli and inter-trial interval as well as two examples of the stimuli used: neutral concordant and threatening discordant. Please note that luminosity of non-black elements (fixation, digits, wheel and spider) has been increased about 100% so they are easier to view (a figure showing original luminosities as presented in the experiment is available at [www.uam.es/CEACO/sup/LuzAmb15.htm](http://www.uam.es/CEACO/sup/LuzAmb15.htm)).

**Figure 2.** Grand averages corresponding to electrodes were relevant components (P1p, P2a, P3o) were most prominent. Locations in red were those quantified and analyzed for P2a; blue locations were those quantified and analyzed for P1p and P3o.

TH=Threatening High mesopic, NH=Neutral High mesopic, TL=Threatening Low mesopic and NL=Neutral Low mesopic conditions.