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**Magnocellular bias in exogenous attention to biologically salient stimuli as
revealed by manipulating their luminosity and color**

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Abstract

Exogenous attention is a set of mechanisms that allow us to detect and reorient towards salient events -such as appetitive or aversive- that appear out of the current focus of attention. The nature of these mechanisms, and particularly the involvement of the parvocellular and magnocellular visual processing systems, was explored. Thirty-four participants performed a demanding digit categorization task while salient (spiders or *S*) and neutral (wheels or *W*) stimuli were presented as distractors under two figure-ground formats: heterochromatic/isoluminant (exclusively processed by the parvocellular system, *Par* trials) and isochromatic/heteroluminant (preferentially processed by the magnocellular system; *Mag* trials). This resulted in four conditions: *SPar*, *SMag*, *WPar*, *WMag*. Behavioral (reaction times and error rates in the task) and electrophysiological (event-related potentials -ERPs-) indices of exogenous attention were analyzed. Behavior showed greater attentional capture by *SMag* than by *SPar* distractors and enhanced modulation of *SMag* capture as fear of spiders reported by participants increased. ERPs reflected a sequence from magnocellular-dominant (*P1p*, ≈ 120 milliseconds) to both magno- and parvocellular processing (*N2p* and *P2a*, ≈ 200 milliseconds). Importantly, amplitudes in one *N2p* subcomponent were greater to *SMag* than to *SPar* and *WMag* distractors, indicating greater magnocellular sensitivity to saliency. Taking together, results support a magnocellular bias in exogenous attention towards distractors of any nature during initial processing, a bias that remains in later stages when biologically salient distractors are present.

Introduction

Salient stimuli, both aversive and appetitive, tend to capture attention more efficiently than anodyne or neutral ones even when they are presented as distractors while the individual is engaged in a cognitive resource-consuming task (Öhman, 1992; Pourtois, Schettino, & Vuilleumier, 2013; Vuilleumier, 2005). This efficiency relies on exogenous attention, also named automatic, stimulus-driven or bottom-up attention among several other terms, which can be conceptualized as our capability to automatically detect and reorient attention to salient events that appear out of the current focus of attention (Yantis, 1993). A frequent experimental strategy to explore exogenous attention is employing concurrent but distinct target-distractor (CDTD) tasks, in which targets (i.e., task relevant elements) and distractors (i.e., task irrelevant) are presented at the same time but are physically segregated so reorienting processes are facilitated (Carretié, 2014). Behaviorally, capture of exogenous attention by distractors in CDTD tasks causes disruption in the ongoing task, which is reflected in poorer processing of concurrent targets: reaction times and/or errors in the response to targets increase (de Fockert, Rees, Frith, & Lavie, 2004; Hickey, McDonald, & Theeuwes, 2006; Theeuwes, 1992). Event-related potentials (ERPs) reflect exogenous attention through enhanced amplitudes in several components, mainly in posterior P1 (P1p), anterior P2 (P2a), and the family of posterior N2 components (N2p) (P1p: Hopfinger & Mangun, 2001; P2a: Kenemans et al., 1989; 1992; N2p: Folstein & Van Petten, 2008; Pazo-Álvarez et al., 2003).

Mechanisms sustaining exogenous attention, favored by evolution as a critical tool for survival, are far from being fully understood. In the visual domain, a relevant mechanism needing further exploration is the contribution of the two main visual processing systems. 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 & Hubel, 1987). Magnocellular and parvocellular LGN neurons also project to separate layers of the striate cortex (Hubel & Wiesel, 1972). Then, parvo- and magnocellular inputs are integrated in the extrastriate cortex (Felleman & Van Essen, 1991; Merigan & Maunsell, 1993). Functionally, parvocellular and magnocellular systems are heterogeneous in their capability to process different visual parameters. The former is more sensitive than the latter to color, higher spatial frequencies, lower temporal frequencies, and has lower luminosity contrast sensitivity; the magnocellular system is more sensitive to luminosity changes, lower spatial frequencies, higher temporal frequencies, has higher contrast sensitivity and is more involved in motion processing (Derrington & Lennie, 1984; DeYoe & Van Essen, 1988; Maunsell & Newsome, 1987; Schiller & Malpeli, 1978).

Several studies suggest that parvo- and magnocellular processing systems may be unequally involved in exogenous attention to biologically salient stimuli. Although this area of research is being incipiently explored, some visual parameters such as spatial frequency and motion have already been studied at this respect. As regards the former parameter, the key role of low spatial frequencies in the detection of biologically salient events (such as threat; Gao, LoBue, Irving, & Harvey, 2016), has been confirmed in exogenous attention studies. Thus, enhanced behavioral and/or neural indices of exogenous attention towards salient distractors -as compared to neutral, anodyne stimuli- have been reported even when high spatial frequencies are eliminated, this enhancement being neutralized when distractors are manipulated to exclusively present high spatial frequencies (Carretié et al., 2012; Vuilleumier et al., 2003). Convergently, and in line with studies showing enhanced fear and freezing responses to dynamic threatening stimuli (Courtney et al., 2010; Sagliano et al., 2014), existing data show that dynamic negative stimuli grab attention to a greater extent than both dynamic non-emotional events and static emotional events (Carretié et al., 2009; Vrijssen et al., 2009).

Greater involvement of the magnocellular visual processing system in saliency detection is probably related to the fact that it directly distributes the information it conveys to crucial areas -other than visual cortices- not reached by the parvocellular system, including those in charge of rapidly evaluating the saliency of stimulation and to organize a response, such as the ventral prefrontal (or orbitofrontal) cortex (Bar et al., 2006; Kveraga et al., 2007), the amygdala (Adolphs, 2004; Vuilleumier, 2005), or the insula (Rodman & Consuelos, 1994).

As indicated, color and luminosity are visual parameters heterogeneously processed by parvo- and magnocellular systems. Thus, while 90% of neurons in the parvocellular layers of the lateral geniculate nucleus are sensitive to different, specific wavelengths (i.e., to specific colors), the remaining 10% of parvocellular geniculate cells and 100% of cells in the magnocellular geniculate layers are not (Livingstone & Hubel, 1988). Each of these “color-blind” cells are sensitive to all wavelengths, so they are especially sensitive to luminosity irrespective of color. Therefore, a figure represented in one color (e.g., red) over a ground with a different but isoluminant color (e.g., green) will not be processed by the magnocellular system (Figure 1). In other words, any brain response that varies between different heterochromatic / isoluminant figure-ground stimuli would reflect parvocellular-originated neural activity; contrarily, brain responses discriminating isochromatic / heteroluminant figure-ground stimuli would mostly reflect magnocellular activity (but not exclusively since, as explained, 10% of parvocellular geniculate cells are also sensitive to luminosity and not to color).

Despite the above mentioned clues suggesting a key role of the magnocellular visual processing system in exogenous attention to biologically salient stimuli and the clear usefulness of manipulating color and luminosity to explore this issue, no data exist, to the best of our knowledge, comparing the neural response to heterochromatic / isoluminant (i.e., “parvocellularly biased”) and to isochromatic / heteroluminant (“magnocellularly biased”)

figure-ground stimuli presented as biologically salient and neutral visual distractors. These two categories will be labeled hereafter as *Par* and *Mag*, respectively, in order to simplify. Our main objective was to explore this issue and, to that aim, participants were faced with a salient (spider) and a neutral distractor (wheel), which were either a red figure over a green isoluminant ground -Par- or a black figure over a grey background (i.e., heteroluminant and isochromatic, since the balance of wavelengths corresponding to different colors was the same in figure and ground) -Mag-. These distractors were presented during a digit categorization CDTD task. Both behavioral and electrophysiological (ERP) indices of exogenous attention were recorded.

We hypothesized an advantage of Mag over Par salient stimuli to capture attention. At the behavioral level, greater interference of salient Mag distractors in the ongoing task was expected, causing greater error rates and/or reaction times. At the neural level, P1p, P2a, and/or N2p components of ERPs, which are sensitive to exogenous attention as mentioned above, were expected to show increased amplitude in response to salient Mag distractors also indexing their advantage to capture attention. Additionally, and as a second objective, this study was interested in exploring the magnocellular / parvocellular balance in global exogenous attention to distractors regardless of their saliency by manipulating distractor luminance and color. This is a relevant but controversial issue that has not been explored through ERPs in CDTD tasks. Indeed, several behavioral studies exploring exogenous attention to (non-emotional) distractors have reported that figure-ground isoluminant color changes are not capable to capture attention (Cole et al., 2005; Irwin et al., 2000; Theeuwes, 1995), but studies exist showing indices of exogenous attention to isoluminant color changes, suggesting a parvocellular contribution (Lu, 2006; Snowden, 2002; Yantis & Hillstrom, 1994). We expected that neural activity revealed by ERPs (not always reflected in the -single- final behavioral output) would shed light on this

issue due to their potential capability to discriminate latencies and/or brain areas showing (or not) a magnocellular bias.

Methods

Participants

Thirty-eight individuals participated in this experiment, although data from only 34 of them could eventually be analyzed, as explained later (28 women, age range of 17 to 48 years, mean=21.35, SD=6.81). The study had been approved by the Universidad Autónoma de Madrid's Ethics Committee. All participants were students of Psychology, provided their informed consent, and received academic compensation for their participation. They reported normal or corrected-to-normal visual acuity.

Upon their informed consent, participants scored their fear level of spiders on a 1 (nil fear) to 10 (maximum fear) scale of fears of 10 different animals, objects and situations (average fear of spiders was 6.61, SD=3.07). As explained below, individual scores were taken into account in data analysis.

Stimuli and procedure

Participants were placed in an electrically shielded, sound-attenuated room. They were asked to place their chin on a chinrest maintained at a fixed distance (60 cm) from the screen (VIEWpixx®, 120 Hz) throughout the experiment. According to the type of distractor, four types of stimuli were presented to participants (Figure 1): biologically salient (spider or S) and neutral distractors (wheel or W), which were either Par (red figure over green ground: heterochromatic/isoluminant condition), or Mag (black figure over grey background: isochromatic/heteroluminant condition). Therefore, four conditions were implemented: SPar, WPar, SMag, and WMag. The size of distractors (figure + ground) was 7.5° x 7.5° width. Details on the physical characteristics of the spider and the wheel used as distractors (i.e., figure-ground luminosities –theoretical/graphical and real as measured through a TES-137®

luminance meter-, RGB saturations, figure surface against background and spatial frequencies), as well as stimuli themselves, are provided in <http://www.uam.es/CEACO/sup/IsoLum17.htm>. As may be appreciated, both spatial frequencies and global figure + ground luminosities were set to be similar across the four conditions since large differences in both parameters have been reported to modulate responses to emotional/salient stimuli (spatial frequency: Delplanque et al., 2007; brightness: Lakens et al., 2013).

Taking into account that the majority of visual ERP components show enhanced amplitudes in response to lateral peripheral stimuli (Capilla et al., 2016; Clark et al., 1994; Eimer, 1996), and with the aim of facilitating differential ERP activity in response to targets, which were symmetrically presented, and to distractors, these were always presented in the left lateral periphery.

*** Figure 1 about here ***

As shown in Figure 1, and along with the distractor, each trial contained two blue central digits (2.5° height), and a blue fixation diamond ($1.25^\circ \times 1.25^\circ$). Distance from the inner border of digits and from the inner border of the distractor square to the center of the fixation diamond -which appeared in the center of the screen- was 2° and 4.8° respectively. The task was related to these central digits: 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 central digit was even and the other was odd (i.e., if they were “discordant”). There were 32 combinations of digits in all, half of them concordant and the other half discordant. In order to ensure that task demands were the same for SPar, WPar, SMag and WMag, these 32 combinations were repeated across the four experimental conditions. Therefore, 128 trials were presented. Stimuli were presented in random order. Participants were instructed to look continuously at the fixation mark. Each picture (containing digits, fixation and distractor) was displayed on the screen for 275 milliseconds, and stimulus

onset asynchrony was 2500 milliseconds.

Recording and pre-processing

Electroencephalographic (EEG) activity was recorded using an electrode cap (ElectroCap International) with tin electrodes. Fifty-nine electrodes were placed at the scalp following a homogeneous distribution and the international 10-20 system. 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 high-pass filter of 0.3Hz¹ was applied. Recordings were continuously digitized at a sampling rate of 420 Hz. An offline digital Butterworth bandpass filter (order: 4, direction: zero phase forward and reverse –twopass- filter) of 0.3 to 20 Hz was applied to continuous (pre-epoched) data using the Fieldtrip software (<http://fieldtrip.fcdonders.nl>; Oostenveld et al., 2011). The continuous recording was divided into 1000 millisecond epochs for each trial, beginning 200 milliseconds before stimulus onset.

EEG epochs corresponding to trials for which subjects responded erroneously or did not respond were eliminated. Ocular artifact removal was carried out through an independent component analysis (ICA)-based strategy (Jung et al., 2000), as provided in Fieldtrip. 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 epoch was discarded. This incorrect response and artifact rejection procedure led to the average admission of 23.87 (SD=3.080) SPar trials, 22.94 (2.461) WPar, 23.32 (2.421) SMag, and 23.06 (2.486) WMag, the difference among conditions being non-significant ($F(3,99) < 2.7$, Greenhouse-Geisser ϵ corrected $p=0.058$, $\eta^2_p=0.075$). The minimum number of trials accepted for averaging was 20 trials per participant and condition. Data from one participant were eliminated since he/she did

¹ The period and frequency of P1, P2a or N2p, the components in which we were interested a priori, is <0.2 s and >8 Hz, respectively, so a low pass 0.3 Hz analog filter leaves an important margin to correctly record the three components avoiding very low-frequency activity to alter the analog signal.

not meet this criterion. The rest of non-analyzed participants (three) presented non solvable anomalies in the recordings of one or more EEG leads (the integrity of all channels was necessary for spatial analyses described later). Beyond these correction/rejection strategies, and in order to discard any significant influence of horizontal ocular activity towards distractors on potential experimental ERP effects, a repeated-measure analyses of variance (ANOVA) introducing Visual Manipulation (Par, Mag) and Biological Saliency (Neutral, Salient) as factors was performed on horizontal EOG data. No significant effects were observed among the latency range of the observed ERP effects -up to 240 ms- ($F(1,33) = 0.102$, $p = 0.751$, $\eta^2_p = 0.003$; $F(1,33) = 0.133$, $p = 0.717$, $\eta^2_p = 0.004$; $F(1,33) = 0.155$, $p = 0.697$, $\eta^2_p = 0.005$, for Visual Manipulation, Biological Saliency, and its interaction, respectively). Later latencies - from 240 ms- did not reveal any effect either ($F(1,33) = 0.260$, $p = 0.614$, $\eta^2_p = 0.008$; $F(1,33) = 0.904$, $p = 0.349$, $\eta^2_p = 0.027$; $F(1,33) = 1.202$, $p = 0.281$, $\eta^2_p = 0.035$, for Visual Manipulation, Biological Saliency, and its interaction, respectively).

Data analysis

Detection, spatiotemporal characterization, and quantification of relevant ERP components

Detection and quantification of P1p, P2a and N2p was carried out through a covariance-matrix-based *temporal* principal components analysis (tPCA), a strategy that has repeatedly been recommended for these purposes (e.g., Chapman et al., 2004; Chapman & McCrary, 1995; Dien, 2010). In brief, tPCA computes the covariance between all ERP time points, which tends to be high between those involved in the same component and low between those belonging to different components. Once quantified in temporal terms, P1p, P2a and N2p topography at the scalp level was decomposed into its main spatial regions via a *spatial* PCA (sPCA) performed on temporal factor scores. sPCA provides a reliable division of the scalp into different regions or spatial factors. Basically, each spatial factor is formed with the scalp points where recordings tend to covary. Temporal and spatial factor scores are the parameters in which temporal and

spatial factors can be quantified, and are linearly related to amplitudes. The decision on the number of factors to select both in tPCA and sPCAs was based on the scree test (Cliff, 1987). Extracted factors were submitted to promax rotation in both cases (Dien, 2010).

Analyses on experimental effects

With respect to behavior, performance in the digit categorization task was analyzed and compared among conditions through two parameters: error rate, defined as the proportion of incorrect responses (0 to 1), and reaction times (RTs) in trials in which participants responded correctly and after discarding those trials in which participants responded three standard deviations below or above their individual RT mean (mean percentage of discarded trials per subject and condition: 1.33%, SD=0.78%). To this end, non-parametric contrasts were carried out (Wilcoxon signed-rank test), because these two variables were not normally distributed (Shapiro-Wilk test: RTs= 0.978, $p = 0.028$; error rate= 0.958, $p < 0.001$). These tests allowed for pairwise contrasts among the four experimental conditions (SPar, WPar, SMag, WMag). Effect sizes in these Wilcoxon contrasts were computed using the procedure described by Pallant for this non-parametrical test (2007, p. 224-225). Additionally, the influence of fear of spiders score (see Participants section) was analyzed, as an index of saliency, via multiple linear regression analyses in order to keep the continuous nature of this parameter. Robust regression analyses were carried out to this aim since they are recommended over standard parametric (least squares) linear regression when cases do not fit gaussian distributions (Huber, 1972). We employed an iterative re-weighted least squares estimation as implemented in the RLM procedure available within the MASS package (Ripley et al., 2016) for R (R Core Team, 2017) using the Huber (1981) weights. Two robust regressions were carried out. In both, the dependent variable was Fear of Spiders, the independent variables being Reaction Times in each condition (sPar, sMag, wPar, wMag) in one of the analyses and Error rates also in each of the four experimental conditions in the other.

With respect to *ERPs*, experimental effects on P1p, P2a and N2p were tested by introducing Visual Manipulation (Par, Mag) and Biological Saliency (Neutral, Salient) as within-subject factors in repeated-measures ANOVAs. Effect sizes in these ANOVAs were computed using the partial eta-square (η^2_p) method. Post-hoc comparisons to determine the significance of pairwise contrasts in potential interactions were performed using the Bonferroni correction procedure. As in the case of behavior, the effect of Fear of Spiders was analyzed via linear multiple regression analyses. In this case, the standard parametric (least squares) procedure was employed, since P1p, P2a and N2p factor scores followed the normality requisite. A multiple regression analyses was carried out for each component introducing Fear as dependent variable and factor scores (amplitudes) in the four experimental conditions (sPar, sMag, wPar, wMag) as independent variables or predictors. The Enter method was employed.

Results

Detection, spatiotemporal characterization and quantification of ERP components

Figure 2A shows a selection of grand averages after subtracting the baseline (prestimulus) activity from each ERP. These grand averages correspond to middle frontal and lateral parieto-occipital areas, where the experimental effects, discussed later, were most prominent. Two important patterns of response already observable in the grand averages are worth mentioning: on the one hand, P1p, P2a and N2p appear to be sensitive to the experimental treatment and, on the other, P2a and N2p overlap in time.

The first analytical step consisted in detecting and quantifying these components through tPCA (see section on Data Analysis). Nine temporal factors (TF) were extracted by tPCA and submitted to promax rotation (Figure 2B). Factor peak-latency and topography characteristics revealed TF2 and TF1 as the critical components, since the former was associated with P1p (peak latency \approx 120 milliseconds) and the latter with P2a and N2p (\approx 180/200 milliseconds). Next, sPCAs applied to the two temporal factors decomposed TF1 into

six spatial factors (SFs) or regions and TF2 into three SFs (Figure 2C). The SF score (equivalent to amplitude, as previously explained) of each SF was extracted per subject and condition.

*** Figure 2 about here ***

Experimental effects

Behavior: Error rate and RTs

Error rate and RTs in the digit categorization task are shown in Table 1. Non-parametric contrasts were performed due to non-normality (see section on Data Analysis). The four conditions (SPar, WPar, SMag, and WMag) were submitted to the Wilcoxon signed-rank test. Error rates were significantly greater in response to SMag than to SPar ($Z=-2.202$, $p=0.028$, effect size or $r=-0.267$), the rest of pairwise contrasts being non-significant ($p>0.078$ in all cases). Additionally, and as explained in Data Analysis section, the effect of Fear of Spiders on behavior was analyzed via robust regressions. These analyses showed a significant and positive relationship between Fear of Spiders and SMag both with respect to error rates ($t(29)=2.582$, $p=0.015$) and to reaction times ($t(29)=2.111$, $p=0.044$): both increased as Fear increased. A negative association between Fear and SPar was also observed in both behavioral parameters (error rates: $t(29)=-2.563$, $p=0.016$, reaction times: $t(29)=-2.606$, $p=0.014$), which increased as Fear decreased. Behavioral results involving WPar and WMag were non-significant ($p>0.29$ in all cases).

*** Table 1 about here ***

ERPs: P1p, P2a and N2p

Experimental effects on all spatial factors into which TF1 and TF2 were decomposed were analyzed, since pre-selecting which of them reflected P1p, P2a and N2p was not a straightforward task (e.g., as explained below, three spatial factors fitted the label “N2p”). Whereas only those spatial factors showing significant effects of Visual Manipulation,

Biological Saliency, or their interaction, will be described in the main text (and are represented in Figure 3), Table 2 shows the mean and the standard error of means of all spatial factor scores (equivalent to amplitudes, as indicated) derived from TF2 (P1) and TF1 (P2/N2) as well as ANOVA results.

First, regarding TF2 (P1), ANOVAs yielded significant results in SF3, a spatial factor presenting parieto-occipital contralateral (to distractor hemifield) distribution (Figure 2C) and that corresponded to **P1p** (this label will be applied to TF2-SF3 hereafter to make results easier to understand). Concretely, main effects of Visual Manipulation on P1b were significant ($F(1,33)=5.104$, $p=0.031$, $\eta^2_p=0.134$), maximal amplitudes being elicited by Mag trials (Figure 3). Neither the main effect of Biological Saliency nor its interaction with Visual Manipulation resulted significant (Table 2).

Second, analyses on TF1, which integrated both P2a and N2p due to their equal latency (but different scalp distribution), also revealed significant effects. On the one hand, analyses on SF1, presenting fronto-central bilateral distribution (Figure 2C), and associated with **P2a** (this label will be applied to TF1-SF1 hereafter), revealed main effects of Visual Manipulation ($F(1,33)=7.620$, $p=0.009$, $\eta^2_p=0.188$). In this case, maximal amplitudes were elicited by Mag trials (Figure 3). The effects of Biological Saliency and the interaction were not significant (Table 2).

On the other hand, three of the spatial factors into which TF1 was decomposed by sPCA, SF2, SF3 and SF6, were associated with three **N2p** subcomponents: one bilateral (N2pb hereafter), one contralateral (N2pc) and one ipsilateral (N2pi), respectively (Figure 2C). It is important to note that these labels are purely descriptive rather than conceptual (e.g., the label “N2pc” strictly describes the polarity –negative-, order -second negativity- and scalp maximum -posterior contralateral- of this subcomponent, but it does not refer to the classical N2pc, usually presenting longer latencies and obtained under bilateral stimulation conditions). These

three spatial factors were sensitive to the experimental effects (Figure 3). Two of them, N2pb and N2pc, were sensitive to Visual Manipulation (N2pb: $F(1,33)=8.510$, $p=0.006$, $\eta^2_p=0.205$; N2pc: $F(1,33)=13.977$, $p=0.001$, $\eta^2_p=0.298$), the greatest amplitudes being elicited by Mag in the case of N2pb and by Par in N2pc (please note that greater amplitudes mean more negativity in all N2p subcomponents). The third N2p subcomponent, N2pi, was significantly sensitive to the interaction of Biological Saliency and Visual Manipulation ($F(1,33)=6.803$, $p=0.014$, $\eta^2_p=0.171$). Post-hoc Bonferroni comparisons showed two significant pairwise contrasts: i) SMag trials elicited greater amplitudes than WMag ($p=0.040$), differences being non-significant between SPar and WPar ($p=0.076$), ii) SMag elicited greater amplitudes than Spar ($p=0.006$), while WMag versus WPar did not reach significance ($p=0.533$).

As indicated in the Data Analysis section, the effect of Fear of Spiders on P1p, P2a, N2pb, N2pi and N2pc was also explored via multiple regression analyses, one for each component, introducing fear of spiders scores as dependent variable. Neither the global regression models nor the coefficients of individual predictors (SPar, SMag, WPar, WMag) reached significance ($p>0.102$ in all cases) in any component.

*** Table 2 about here ***

Relationship between behavior and ERPs

In order to test the linkage between behavior and critical ERP components, a multiple regression analysis was carried out using the Enter method. Error rate, the behavioral parameter showing sensitivity to the experimental treatment in non-parametric, was introduced as the dependent variable. On the other hand, the amplitude (i.e., spatial factor scores) of those components reaching significant differences among conditions -P1p, P2a and N2p subcomponents (N2pb, N2pc and N2pi)- were introduced as predictor variables. The regression model was shown to be significant (corrected $R^2 = 0.087$, $F(5,130) = 3.558$, $p=0.005$).

Coefficients of individual predictors showed a strong association of Error rate with N2pb (beta = -0.328, $p < 0.001$), indicating that greater amplitudes (i.e., more negative) in this subcomponent of N2p were associated with higher error rates. The rest of individual predictor coefficients did not reach significance ($p > 0.158$ in all cases).

Discussion

Our first objective was to study the parvo / magnocellular balance in exogenous attention to biologically salient distractors, and our second scope was exploring the parvo / magnocellular balance on global exogenous attention to distractors regardless of their saliency. Present results support a magnocellular bias in exogenous attention towards distractors of any nature during initial processing, a bias that remains in subsequent processing when biologically salient distractors are present. These general conclusions derive from a set of specific findings that can be summarized, integrating both objectives, as follows: i) the initial visual responses to distractors (≈ 100 milliseconds) are mainly mediated by the magnocellular processing system, ii) the subsequent chronological phase (≈ 200 milliseconds) reflects parvocellular processing along with magnocellular, iii) this second phase, and concretely its magnocellular constituent, would be specially involved in the detection of biological saliency (as reflected in N2pi) and would significantly associate with behavioral indices of exogenous attention (N2pb). Next, this chronological sequence will be discussed in detail.

The parvo/magnocellular processing balance began with a net magnocellular processing dominance, relative to parvocellular, at around 120 milliseconds from stimulus onset, since P1p showed significantly greater amplitudes in response to isochromatic/heteroluminant figure-ground distractors (Mag trials) than to heterochromatic/isoluminant (Par trials). This is in accordance with previous data showing a P1p magnocellular pattern of processing in response to stimuli presenting different contrast levels (Ellemberg et al., 2001). Whereas it is indubitable that P1p is reflecting processing of distractors, whether it reflects (exogenous) attentional or

purely perceptual mechanisms needs additional discussion. P1p has been reported to reflect perceptual differences associated with the mere visual dissimilarities among conditions. For example, P1p has shown to be sensitive to global brightness of stimuli (Paulus et al., 1984). However, in our opinion this is improbable in the present case. As indicated in the Methods section, global luminosity and spatial frequency of distractors (figure + ground) was similar. Color of distractors was of course different among Par and Mag trials, but, to the best of our knowledge, no studies have shown net perceptual effects of color (i.e., color effects not mediated by task instructions, such as attending to one particular color and ignoring others). On the contrary, data exist showing P1p insensitivity to this parameter (Paulus et al., 1984). The rest of parameters (sizes of distractors and digits, global screen brightness, figure forms) were completely homogenous across conditions. On the other hand, P1p has been previously associated with cognitive processes beyond perception (importantly, with attentional capture: Hopfinger & Mangun, 2001). In any case, this issue is worth exploring in future studies.

The second chronological phase involves two parallel processes peaking almost at the same time and involved in the same temporal factor extracted by tPCA, one reflected in N2p (≈ 180 milliseconds), and the other, peaking slightly later in grand averages, reflected in P2a (≈ 200 milliseconds). The former (N2p), was subdivided by sPCA into three spatial subcomponents: N2pb (bilateral), N2pc (contralateral to the distractor hemifield and unrelated to traditional N2pc, as indicated above) and N2pi (ipsilateral). Globally, these subcomponents revealed again magnocellular-biased processing, but parvocellular also came significantly into play at this step. Thus, while N2pb showed greater amplitudes to isochromatic/heteroluminant (Mag) distractors, N2pc amplitude was maximal in response to the heterochromatic/heteroluminant (Par) distractors. Importantly, the third N2p subcomponent, N2pi, did not show a main effect of visual manipulation, but an interaction of this factor with biological saliency: salient stimuli elicited significantly greater amplitudes than neutral only

among Mag trials (differences were not significant among Par trials). Moreover, salient Mag distractors elicited greater N2pi amplitudes than salient Par ones. In other, more graphical words, the magnocellular channel showed greater sensitivity to saliency than the parvocellular channel. These results were in line with behavioral data. Indeed, error rates in the ongoing digit categorization task were greater to salient Mag than to salient Par distractors. Additionally, both error rates and reaction times increased in response to salient Mag as fear of spiders increased, an index of saliency. This direct relationship was absent in salient Par trials (an inverse relationship was even observed in this case).

As indicated above, N2p has been previously found to show enhanced amplitudes in response to stimuli capturing exogenous attention (see reviews in Folstein & Van Petten, 2008; Pazo-Álvarez et al., 2003). As in the present N2pi, emotional distractors enhance N2 amplitudes as compared to neutral distractors (Buodo et al., 2010; Carretié et al., 2004; 2013b; Eimer & Kiss, 2007; Feng et al., 2012; López-Martin et al., 2013). The ipsilateral (along with bilateral and contralateral) cortical contribution to N2p is in line with previous data showing the involvement of the ipsilateral visual cortex in attentional processes (Loughnane et al., 2016). In this same vein, N2p has shown ipsilateral occipito-temporal N2 increased amplitudes during exogenous attention to magnocellular-biased stimuli (moving deviants: Pazo-Álvarez et al., 2004).

Parallel to the N2p process, the second step involves P2a, a bilateral, fronto-centrally distributed component peaking approximately at 205 milliseconds. This component has been reported to be a neural index of exogenous attention (Kenemans et al., 1989; Kenemans et al., 1992), and present results suggest that it preferentially reflects the parvocellular part of this process since maximal P2a amplitudes were elicited by Par distractors. In line with these results, previous data indicate that P2a is insensitive to magnocellular stimulus characteristics such as direction of motion (Hoffmann et al., 2001). Previous studies have shown increased

P2a amplitudes in response to salient/emotional distractors (Carretié et al., 2013b; Feng et al., 2012; Holmes et al., 2006; Junhong et al., 2013), but despite it showed maximal amplitudes in response to salient Par stimuli, saliency effects did not reach significance in the present experiment. Exploring parameters that modulate P2a sensitivity to saliency, such as visual complexity (pictures instead of silhouettes are usually employed in the studies mentioned above), seems necessary in future studies on this consistently useful index of exogenous attention.

It is important to indicate that at least part of the observed effects, in this and other experiments on exogenous attention, could lie in spatial competition of targets and distractors (both are spatially close, in terms of visual angles, in the majority of CDTD studies: see reviews in Carretié, 2014; Corbetta et al., 2008). Thus, whereas targets and distractors were physically segregated in the present experiment, they could overlap, at least partially, in the same receptive field of certain neurons of the visual cortex, mainly at those regions of the ventral extrastriate cortex where receptive fields of individual neurons are larger (i.e., V4 and TEO; see Smith et al.; 2001, for a characterization of the receptive fields of several visual cortex regions, including V4). This spatial competition causes a complex “biased competition” or “push–pull” pattern of neural activity consisting of inhibiting or suppressing the irrelevant visual stimuli that compete in the same receptive field with the relevant stimulus, whose processing is enhanced (Beck & Kastner, 2005; Desimone, 1998; Kastner & Pinsk, 2004; Kastner & Ungerleider, 2000; Miller et al., 1993; Reynolds et al., 2000). Thus, when top-down mechanisms prioritizes one of these stimuli as being task relevant -target- and the others become task irrelevant -distractors-, the neural response to the former is as strong as if presented alone (Chelazzi, Duncan, Miller, & Desimone, 1998; Desimone, 1998). From this perspective, enhanced neural activity usually observed in response to salient distractors would be due, at least in part, to an enhanced push-pull conflict in situations in which top-down

relevance (targets) and bottom-up relevance (salient distractors) compete in the same space. Whereas manipulation of eccentricities reveal that the ERP effects of biased competition between targets and salient distractors are manifested later in time (from 300 ms: see Carretié et al., 2013a), this is a crucial issue that needs further exploration.

A final comment deals with the controversy mentioned in the Introduction regarding behavioral data on exogenous attention to (non-emotional) distractors that have previously manipulated color and luminosity. As indicated, isoluminant color changes were not capable to capture attention in some studies (Cole et al., 2005; Irwin et al., 2000; Theeuwes, 1995), but were capable in others (Leonard & Luck, 2011; Yantis & Hillstrom, 1994), pointing to a significant parvocellular involvement. Behavioral results in our experiment showed Mag>Par differences in response to salient stimuli, but they did not reach significance in response to neutral stimuli. Nevertheless, error rates were significantly associated with the magnocellular-sensitive N2p subcomponent (N2pb). Therefore, present behavioral results lead to mixed conclusions. Employing a cue-target paradigm instead of a CDTD task, Ries and Hopfinger (2011) also reported ERP data regarding P1 and P3 that supported the contribution of parvo- along with magnocellular processing in exogenous attention. Present ERP results, namely those on N2pc and P2a, confirm the contribution of the parvocellular system. However, they also show that, at least using CDTD tasks (i.e., both targets and distractors concurred), a net magnocellular bias is produced in initial latencies (P1p). Moreover, and connecting with the first scope of this study, this magnocellular bias remains in later stages towards some specific distractor contents, as revealed by N2pi results. Behavior, which is the single final output of a complex set of neural processes, reflected mainly this magnocellular bias to saliency in our study, but it could probably reflect different processes as a function of the experimental design, tipping the parvo/magnocellular balance to one side or the other. Therefore, ERPs seem an especially valuable tool to disentangle the effects observed at the behavioral level in this field

of research.

In sum, results reveal a magnocellular bias in exogenous attention to distractors of any nature during initial processing, a bias that remains in later stages when biologically salient distractors are present. It is worth noting that a magnocellular bias has been also reported in ERP studies where participants *endogenously* attend to emotional stimuli and where spatial frequency and/or color characteristics are manipulated (e.g., Alorda et al., 2007; Carretié et al., 2007; Miskovic et al., 2015; Pourtois et al., 2005). Consequently, current ERP studies suggest a key role of the magnocellular system in global attentional processes (both exogenous and endogenous) towards affective visual events. Future ERP research is needed to further explore magnocellular and parvocellular roles in exogenous attention to salient events trying to overcome potential limitations of the present experiment. Thus, raising the number of trials in order to increase the signal-to-noise ratio but, in parallel, avoiding the potential differential effect of habituation on salient versus neutral stimulus repetition when a large number of trials is employed (see Carretié et al., 2003; Codispoti et al., 2007) would be advisable. Moreover, introducing more stimulus exemplars for each experimental category would be of interest to avoid possible effects linked to a particular shape.

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Table 1. Means and standard error of means (SEM) of behavioral responses (error rate and reaction times –RTs-) to each experimental condition (S=spider, W=wheel, Par=heterochromatic / isoluminant, Mag=isochromatic / heteroluminant, High=high fear of spiders group –n=19-, Low=low fear of spiders group –n=15-, All=all participants –n=34-).

		Error rate (0 to 1)		RTs (ms)	
		Mean	SEM	Mean	SEM
SPar	High	0.091	<i>0.016</i>	902.993	<i>34.568</i>
	Low	0.135	<i>0.022</i>	939.003	<i>50.172</i>
	All	0.110	<i>0.013</i>	918.880	<i>29.070</i>
SMag	High	0.128	<i>0.015</i>	906.696	<i>37.913</i>
	Low	0.127	<i>0.021</i>	907.772	<i>50.429</i>
	All	0.127	<i>0.012</i>	907.171	<i>30.234</i>
WPar	High	0.125	<i>0.018</i>	905.916	<i>36.380</i>
	Low	0.118	<i>0.025</i>	936.737	<i>54.769</i>
	All	0.122	<i>0.015</i>	919.513	<i>31.176</i>
WMag	High	0.118	<i>0.017</i>	918.077	<i>35.099</i>
	Low	0.133	<i>0.023</i>	931.200	<i>53.224</i>
	All	0.124	<i>0.014</i>	923.867	<i>30.116</i>

Table 2. Means and standard error of means (SEM) of P1p, P2a and N2p spatial factor scores (equivalent to amplitudes) to each experimental condition and results (F, probability –p- and effect size η^2p -) yielded by the two-way ANOVA involving Distractor and Light factors. Significant results are shown in bold letters (S=spider, W=wheel, Par=heterochromatic / isoluminant, Mag=isochromatic / heteroluminant).

		Means (SEMs)				ANOVAs								
						Visual Manipulation			Saliency			Visual Manipulation x Saliency		
		SPar	SMag	WPar	WMag	F(1,33)	p	η^2p	F(1,33)	p	η^2p	F(1,33)	p	η^2p
TF2	TF2SF1	-0.042 (0.169)	0.103 (0.201)	-0.056 (0.171)	0.012 (0.162)	0.323	0.574	0.01	0.11	0.743	0.003	0.103	0.751	0.003
	TF2SF2	0.034 (0.150)	-0.096 (0.211)	0.062 (0.155)	-0.008 (0.178)	0.991	0.327	0.029	0.477	0.495	0.014	0.004	0.951	0
	TF2SF3 (P1p)	-0.297 (0.190)	0.227 (0.174)	-0.126 (0.168)	0.224 (0.154)	5.104	0.031	0.134	0.52	0.476	0.016	0.403	0.53	0.012
TF1	TF1SF1 (P2a)	0.209 (0.185)	-0.158 (0.176)	0.022 (0.184)	-0.114 (0.149)	7.62	0.009	0.188	0.282	0.599	0.008	0.133	0.718	0.004
	TF1SF2 (N2pb)	0.067 (0.147)	-0.161 (0.181)	0.055 (0.182)	-0.085 (0.166)	8.51	0.006	0.205	0.001	0.969	0	0.136	0.714	0.004
	TF1SF3 (N2pc)	-0.156 (0.182)	0.162 (0.173)	-0.192 (0.178)	0.213 (0.161)	13.977	0.001	0.298	0.485	0.491	0.014	0.443	0.51	0.013
	TF1SF4	0.288 (0.182)	-0.041 (0.155)	-0.066 (0.176)	-0.188 (0.184)	2.107	0.156	0.06	2.587	0.117	0.073	0.384	0.54	0.011
	TF1SF5	0.062 (0.181)	-0.019 (0.202)	-0.051 (0.154)	0.016 (0.164)	0.035	0.853	0.001	0.213	0.647	0.006	0.17	0.683	0.005
	TF1SF6 (N2pi)	0.198 (0.199)	-0.198 (0.162)	-0.024 (0.147)	0.063 (0.186)	2.896	0.098	0.081	0.09	0.766	0.003	6.803	0.014	0.171

Figure legends

Figure 1. Examples of stimuli pertaining to the four experimental conditions (regarding the task, the two example stimuli above are Concordant and those shown below are Discordant). A full scale version of distractors is available at www.uam.es/CEACO/sup/IsoLum17.htm.

Figure 2. A) Grand averages at midline anterior, left posterior and right posterior areas, where P2a and N2p and P1p, respectively, are prominent. B) tPCA: Factor loadings after promax rotation and TF2 (P1p) and TF1 (P2a / N2p) temporal factor scores in the form of scalp maps. C) sPCA: loadings –in the form of scalp maps- of spatial factors in which TF1 and TF2 were decomposed showing significant experimental effects. (S=spider, W=wheel, Par=heterochromatic / isoluminant, Mag=isochromatic / heteroluminant). Scalp maps of spatial factors not showing significant experimental effects are represented in a supplementary figure available at www.uam.es/CEACO/sup/IsoLum17.htm.

Figure 3. Bar diagram representing means and standard error of means (error bars) of spatial factor scores (linearly related to amplitudes) corresponding to those components showing significant experimental effects. Note that, in positive components (green), more positive values mean more amplitude, whereas in negative components (red), more negative values mean more amplitude. Significance corresponds to ANOVA (main effect) results except in N2pi, where the interaction was significant; in this case, significance corresponds to post-hoc Bonferroni contrasts (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.005$). (S=spider, W=wheel, Par=heterochromatic / isoluminant, Mag=isochromatic / heteroluminant).