Differential neural mechanisms underlying exogenous attention to peripheral and central distracters

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Abstract
Mechanisms underlying exogenous attention to central and peripheral distracters were temporally and spatially explored while 30 participants performed a digit categorization task. Neural (event-related potentials—ERPs—analyzed both at the scalp and at the voxel level) and behavioral indices of exogenous attention were analyzed. Distracters were either biologically salient or neutral, in order to test whether the exogenous attention bias to the former observed in previous studies is independent of, or interacts with, distracter eccentricity. Two subcomponents of the N2 component of the ERPs, N2olp and N2ft, reflected processes related to peripheral distracters processing. N2olp effects, located in the dorsal attention network (supplementary motor area), were probably related to covert reorientation to peripheral distracters. N2ft effects, located in the default mode network (posterior cingulate cortex), appeared to reflect less effort in the ongoing task when peripheral distracters were presented. N2ft also showed a biological saliency effect which was independent of eccentricity and was located in the polar ventral prefrontal cortex. P3 showed greater amplitudes to centrally presented distracters. These latter effects were located in TEO (visual cortex), and would be functionally associated with spatial interference between the target and central distracters. Behavior showed the relevance of both central and peripheral distracters in exogenous attention. These results indicate that exogenous attention to peripheral distracters differed in temporal and spatial terms from exogenous attention to central distracters and that it is biased towards biologically salient events irrespective of their eccentricity.

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1. Introduction
Exogenous attention, also named automatic, stimulus-driven or bottom-up attention, among other terms, is the process by which a distracter automatically captures our attention diverting it from the task where endogenous (voluntary, controlled or top-down) attention is directed. In other words, events capturing exogenous attention appear outside the current focus of processing. In many situations, they also appear out of the focus of gaze, projecting to non-foveal areas of the retina. In these areas, perception is much poorer than in fovea, mainly due to the fact that density of cones (a type of retinal photoreceptor which is responsible for detecting visual information in day light; e.g., Sterling, 2003) progressively and dramatically drops as eccentricity from fovea increases (more than 10 times in only 5 mm eccentricity; e.g., Jonas, Schneider, & Naumann, 1992; Packer, Hendrickson, & Curcio, 1989). The consequence is that each peripheral cone covers a much wider area of the visual field than each foveal cone, and details (i.e., high spatial frequencies) are lost. At the brain level, central vision is represented more densely in the parvocellular layers of the lateral geniculate nucleus than in the magnocellular layers, while magnocellular density declines more slowly with eccentricity than does parvocellular density (Brown, Halpert, & Goodale, 2005). Consequently, parvocellular information is richer in color and details than magnocellular. Therefore, processing resources need to be reoriented to the peripheral event in order to be better perceived.

In these cases, exogenous attention should be specially linked to the neural mechanisms involved in the reorientation of gaze, head or even body. Indeed, one of the main brain circuits underlying exogenous attention, the dorsal attention network (DAN), engages several superior parietal and dorso-frontal areas that are critical for organizing and controlling eye movements, as well as body reorientation, such as the frontal eye fields, parietal eye fields, or motor and premotor cortices (see reviews in Corbetta, Patel, & Shulman, 2008; Pierrot-Deseilligny, Milea, & Müri, 2004; Posner, Rueda, & Kanske, 2007; Smith & Schenk, 2012). Importantly, areas associated with motor reorienting are recruited even
in covert attention tasks (i.e., those in which attention, but not gaze, must be directed to the peripheral stimulus: Grosbras, Laird, & Paus, 2005).

Nevertheless, these motor reorienting mechanisms are not inherent in exogenous attention. Sometimes, events automatically capturing attention are not peripherally located. They might be detected, for example, close to the currently attended stimulus, or in central positions at different planes (i.e., behind or in front of the attended stimulus). These situations do not necessarily require motor reorientation (i.e., redirection of body, head or even gaze) to process the distracter. However, these central distracters would trigger specific mechanisms that are absent or less prominent in the case of peripheral distracters. For example, they might be more difficult to be ignored /perceptually ‘suppressed’ (in case they are considered irrelevant) or exogenously attended (in case they are considered relevant) than peripheral distracters, since they spatially compete with the endogenously attended target. Spatial competition causes a complex ‘push–pull’ or ‘biased competition’ pattern of neural activity in extrastriate visual areas, mainly at the stages of the visual ventral pathway where receptive fields of individual neurons are larger (i.e, V4 and TEO; for a characterization of these two areas in the human brain, see Kastner et al., 2001). This pattern favours the inhibition of the distracter while enhancing the processing of the target (Beck & Kastner, 2005; Desimone, 1998; Kastner & Pinsk, 2004; Kastner & Ungerleider, 2000; Miller, Gochin, & Gross, 1993; Reynolds, Pasternak, & Desimone, 2000).

Based on the above, it seems reasonable to hypothesize that the neural mechanisms underlying exogenous attention to peripheral distracters might be different from those associated with central distracters. However, evidence of this dissociation is only indirect and scarce up to date. In the present study, and with the aim at exploring this question, distracters were presented at different eccentricities as well as from an evolutionary point of view, it would be reasonable to expect that biological saliency should be detected even for distracters appearing in the periphery. However, the existing literature on this issue does not provide convergent results. While some data show that these stimuli evoke greater attention-related signals than neutral stimuli independently of their eccentricity (emotional facial expressions: Bayle, Henaff, & Krolak-Salmon, 2009; Rigoulot, D’Hondt, Defoort-Dellemmes, Despretz, & Honoré, 2011; Rigoulot, D’Hondt, Honore, & Sequeira, 2012; affective non-facial scenes: Calvo, Nummenmaa, & Hyönä, 2008), others report no differences between biologically salient and neutral distracters when presented in the periphery (i.e., at – 2.21’: De Cesarei, Codispoti, & Schupp, 2009, employing affective scenes as stimuli). To shed light on this question, both neutral and biologically salient distracters were included in the experimental design (non-facial distracters in both cases, since previous literature is specially divergent in this case; see Carretié et al., in press, for a comparison on the effects of facial and non-facial biologically salient stimuli on exogenous attention). In sum, this study aimed to investigate the neural mechanisms underlying exogenous attention to distracters presented at different eccentricities, and whether this factor interacts with biological saliency of distracters.

2. Material and methods

2.1. Participants

Thirty-five individuals participated in this experiment, although data from only 30 of them could eventually be analyzed, as explained later (26 women, age range of 17 to 28 years, mean = 19.65, SD = 2.39). The study had been approved by the Universidad Autónoma de Madrid’s Ethics Committee. All participants were students of Psychology at that university and took part in the experiment voluntarily after providing informed consent. They reported normal or corrected-to-normal visual acuity.

2.2. Stimuli and procedure

Participants were placed in an electrically shielded, sound-attenuated room, and stimuli were presented on a back-projection screen through a RGB projector. They were asked to place their chin on a chinrest maintained at a fixed distance from the screen throughout the experiment. According to the type of distracter, seven types of stimuli were presented to participants: no distracter (D0); biologically salient distracter proximal (Sprox), neutral distracter proximal (Nprox), biologically salient distracter medium eccentricity (Smed), neutral distracter medium angle (Nmed), biologically salient distracter distant (Sdist), and neutral distracter distant (Ndist). The size for all distracters was 5.15 x 5.15 height each), one of these stimuli contained two red central digits (1.33’’ height each), one above the other, their inner borders being at 2.41’, vertically, from the center of the screen. Each stimulus was displayed on the screen for 350 ms, and stimulus onset asynchrony was 3000 ms. The task was related to the 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, half of them concordant and the other half discordant. The same combination of digits was repeated across all eccentricity and biological saliency conditions in order to ensure that task demands were the same for the seven conditions. These 32 x 7 (224) trials of each type were presented in two runs separated by a rest period. Stimuli were presented in semi-random order in such a way that there were never more than five consecutive trials for the same distracter or numerical category. Participants were instructed to look continuously at a fixation mark located in the center of the screen and to blink preferably after a beep that sounded 1300 ms after each stimulus onset. An animation reproducing the stimulation sequence with examples of all experimental conditions is shown in http://www.uam.es/CEACO/sup/visualangle12.htm.

2.3. 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. All scalp electrodes were referenced to the nose tip. 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 10 kHz was applied. Recordings were continuously digitized at a sampling rate of 420 Hz. The continuous recording was divided into 1000 ms epochs for each trial, beginning 200 ms before stimulus onset. Behavioral activity was recorded by means of a two-button keypad whose electrical output was also continuously digitized at a sampling rate of 420 Hz. An offline digital bandpass filter of 0.3 to 30 Hz was applied using the Fieldtrip software (http://fieldtrip.fcdonders.nl; Oostenveld, Fries, Maris, & Schoffelen, 2011).

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 (see a description of this procedure and its advantages over traditional regression/covariance methods in Jung et al., 2000), as provided in Fieldtrip. After the ICA-based removing process, a second stage of ocular artifact rejection was performed on the ICA-cleaned data. Ocular artifacts were detected using a method based on correlation analyses between each electrode and the corresponding horizontal or vertical EOG channel. Bandpass filtering (0.3 Hz to 10 kHz) was applied to adjust degrees of freedom where necessary. 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 Bonferroni correction procedure. The specific characteristics of the analyses according to the nature of the dependent variable were as follows.

(i) Behavior. Performance in the digit categorization task was analyzed. To this end, reaction times (RTs) and error rate (percentage of incorrect responses) in response to each of the seven conditions were submitted to non-parametric contrasts, because these two variables were not normally distributed (RTs: SW = 0.976, p < 0.01; errors: SW = 0.913, p < 0.001). The main scope of this analysis was to test whether distracter conditions (NPerr, NPerr, NMmed, NMmed, NDist, SDist, SDist) showed behavioral indices of exogenous attention when compared with the non-distracter condition (D0). In the case of RTs, outliers, defined as responses over 2000 or below 200 ms, were omitted in the analyses.

(ii) Scalp amplitudes (2D). Experimental effects on N2 and other relevant components at the scalp level (2D) were also tested. Eccentricity (Proximal, Medial, Distal) and Biological Saliency (Neutral, Salient) were introduced as factors in a repeated-measures ANOVA. Prior to analyses, amplitudes in response to D0 were subtracted from the six distracter conditions in every subject in order to discount the effect of target.

(iii) Source (3D) analyses. Temporal factor scores corresponding to relevant components were submitted to exact low-resolution brain electromagnetic tomography (eLORETA). eLORETA is a 3D, discrete linear solution for the EEG inverse problem (Pascual-Marqui, 2002). Although solutions provided by EEG-based source-location algorithms should be interpreted with caution due to their potential error margins, the use of ICA-derived factor scores instead of direct voltages (which leads to more accurate source-localization analyses: Carreté et al., 2004b; Dien, Spencer, & Donchin, 2003) and the relatively large

Fig. 1. Examples of stimuli belonging to several experimental conditions. Only ‘discordant’ examples are shown. D0 (no distracter) stimuli consisted of the two red digits alone.
sample size employed in the present study \(n=30\) contribute to reducing such error margins. Pairwise contrasts at the voxel level between stimulus conditions showing significant differences at the scalp level were computed in order to detect potential sources of variability using the non-parametric mapping (SnPM) tool provided by eLORETA (Nichols & Holmes, 2001). In order to further explore these differences through full factorial contrasts, regions of interest (ROIs) were defined for those sources, and their current densities were exported and submitted to a repeated-measures ANOVA using Eccentricity (Proximal, Medial, Distal) and Biological Salience (Neutral, Salient) as factors. Also in this case and prior to ANOVAs, amplitudes in response to D0 were subtracted from the rest of conditions in every subject in order to discount the effect of target.

3. Results

3.1. Detection, spatiotemporal characterization and quantification of ERP components

Fig. 2 shows a selection of grand averages after subtracting the baseline (prestimulus) activity from each ERP. These grand averages correspond to midline frontal and lateral parieto-occipital areas, where the experimental effects (discussed later) were most prominent. An important pattern of response already observable in the grand averages is that N2 can be decomposed in two different components labeled N2olp and N2ft in this study. The former was maximal at occipital and lateral parietal regions (olp), and its latency was slightly shorter than that of N2ft, maximal at frontal and temporal areas (ft) (see also maps in Fig. 3). Additionally, the wave labeled as ‘P3’ in the grand averages, presenting the typical posterior distribution and following N2, also suggests sensitivity to the experimental manipulations. As a consequence, this component was also analyzed.

The first analytical step consisted in detecting and quantifying these components through tPCA (see section on Data Analysis). Seven temporal factors (TF) were extracted by tPCA and submitted to promax rotation (Fig. 3). Factor peak-latency and topography characteristics revealed TF6, TF8, and TF1 as the critical components, since they were associated with N2olp and N2ft and P3, respectively (Fig. 2). These labels will be employed hereafter to make results easier to understand. sPCA applied to the three temporal factors defined five different spatial factors (SFs) or regions in each case. The SF score (equivalent to amplitude, as previously explained) of each SF was extracted per subject and condition.

3.2. Experimental effects on scalp N2olp, N2ft, and P3 (2D)

As explained above, repeated-measures ANOVAs on Eccentricity (Prox, Med, Dist) x Biological Saliency (Neutral, Salient) were carried out for each spatial factor within each temporal component (N2olp, N2ft and P3), once factor scores to D0 were subtracted from all conditions. According to our main objective, relevant SFs were those in which significant central vs peripheral effects were observed. Table 1 shows means and standard error of the means for N2olp, N2ft and P3 relevant SF scores in the six distracter conditions once those in response to D0 (no distracter) were subtracted.

3.2.1. N2olp

ANOVAs yielded significant results in SF5, presenting bilateral distribution (Fig. 4). Concretely, main effects of Eccentricity were observed \(F(2,58)=12.262, p<0.001, \eta^2_p=0.297\), maximal amplitudes being elicited by Med and Dist eccentricities, which significantly differed from Prox distracters. Neither the main effect of Biological Saliency nor the interaction Eccentricity x Biological Saliency were significant.

3.2.2. N2ft

Main effects of Biological Saliency \(F(1,29)=6.318, p<0.05, \eta^2_p=0.179\) and Eccentricity \(F(2,58)=21.732, G-G \ p<0.001, \eta^2_p=0.428\), but not the interaction, were patent in SF5, characterized by

![Fig. 2. Grand averages at frontal and lateral parieto-occipital areas, where the experimental effects are prominent. The three relevant components are signaled. D0—no distracter, Nprox—neutral distracter proximal, Nmed—neutral medium angle, Ndists—neutral distant, Sprox—biologically salient proximal, Smed—biologically salient medium angle, Sdist—biologically salient distant.](image)
Fig. 3. Temporal factors extracted by tPCA. The three relevant factors are drawn in red, blue and black. Their factor scores in the form of scalp maps are also represented; blue means negative amplitudes and red means positive amplitudes (maps elaborated through eLoreta software: http://www.uzh.ch/keyinst/loreta.htm). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Means and standard error of the means (in parenthesis) of scalp neural responses (factor scores, linearly related to amplitudes) to each distracter type, once responses to the non-distracter condition (D0) was subtracted to each of them. SF = spatial factor.

<table>
<thead>
<tr>
<th></th>
<th>Neutral</th>
<th>Biologically salient</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Proximal</td>
<td>Medial</td>
</tr>
<tr>
<td>N2oLP (SF5)</td>
<td>0.536 (0.169)</td>
<td>-0.180 (0.179)</td>
</tr>
<tr>
<td>N2fT (SF5)</td>
<td>-0.650 (0.146)</td>
<td>0.028 (0.184)</td>
</tr>
<tr>
<td>P3 (SF4)</td>
<td>0.873 (0.228)</td>
<td>0.254 (0.187)</td>
</tr>
</tbody>
</table>

Table 2
Means and standard error of the means (in parenthesis) of behavioral responses (reaction times -RTs- and error rate) to each experimental condition.

<table>
<thead>
<tr>
<th></th>
<th>No distracter</th>
<th>Neutral</th>
<th>Biologically salient</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Proximal</td>
<td>Medial</td>
</tr>
<tr>
<td>RTs (ms)</td>
<td>943.276 (32.388)</td>
<td>987.262 (30.789)</td>
<td>961.001 (33.283)</td>
</tr>
<tr>
<td>Error rate (%)</td>
<td>7.292 (1.220)</td>
<td>6.250 (1.016)</td>
<td>6.563 (0.852)</td>
</tr>
</tbody>
</table>

Fig. 4. Loads of relevant spatial factors in the form of scalp maps in order to illustrate their topography (the more intense the red color, the higher the load). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
a central/midline topography (Fig. 4). In the case of Biological Saliency, amplitudes elicited by salient distracters were greater than those elicited by neutral distracters. In the case of Eccentricity, post-hoc tests showed that the maximal amplitudes (i.e., the most N2ft negative values) were elicited by Prox distracters, which significantly differed from Med and Dist distracters.

3.2.3. P3
ANOVAs yielded significant results in SF4, which presented bilateral distribution (Fig. 4). Differences were produced with respect to Eccentricity ($F(2,58) = 5.257, p < 0.01, \eta^2_p = 0.153$). Maximal amplitudes were elicited by Prox distracters, which significantly differed from Med and Dist distracters according to post-hoc contrasts. No main effects of Biological Saliency nor the interaction Eccentricity x Biological Saliency were observed.

3.3. Experimental effects on 3D sources
3.3.1. Region-of-interest (ROI) analyses
First, and in order to localize the effects observed at the surface level, eLoreta maps were computed for N2olf, N2ft and P3 temporal factor scores per subject and condition. Subsequently, and as explained in the Methods section, several ROIs were defined following data-driven criteria. In the case of N2olf, in which main effects of Eccentricity (Prox distracters eliciting minimum amplitudes) were observed at the surface level, a ROI was defined as those voxels in which maximal Prox < Dist current densities were observed in the SnPM contrasting tool provided by eLoreta (in which only pairwise contrasts are possible). With respect to N2ft, ROIs were those comprising voxels showing the greatest Sal > Neu and Prox > Dist differences, since main effects of both Eccentricity and Biological Saliency were significant at the surface level. Finally, P3 showed Eccentricity effects (proximal distracters eliciting the greatest amplitudes) at the scalp level, so ROIs were configured including those voxels showing maximal Prox > Dist current densities.

Fig. 5 shows the ROIs obtained in the three cases. Current densities within these ROIs in every subject and condition were then quantified through the ad hoc tool provided by eLoreta. Afterwards, and in order to submit these current densities to richer, full factorial statistical constrasts, they were exported and submitted to ANOVAs using Eccentricity (Prox, Med, Dist) and Biological Saliency (Neutral, Salient) as factors after subtracting current densities elicited by D0 condition.

3.3.2. N2olf
A ROI was defined in BA6 (Fig. 5), involving those voxels in which maximal Prox < Dist differential current densities had been

![Fig. 5](image_url)

Fig. 5. ROIs in which current densities were sensitive to the experimental conditions. Average current densities for each condition are also shown (Prox = proximal distracters; Med = medium angle distracters; Dist = maximal angle distracters). Error bars represent standard error of the means.
observed. The main effect of Eccentricity was confirmed by ANOVAs to be significant in this ROI ($F(2,58)=5.456$, $\eta^2_p=0.158$). Post-hoc analyses carried out through the Bonferroni procedure indicated that significant differences were produced between Prox and Dist conditions (Fig. 5). No effect of Biological Saliency (Neutral, Salient) nor the interaction between Eccentricity and Biological Saliency were observed ($p>0.05$).

3.3.3. N2ft

First, the ROI corresponding to voxels showing maximal Sal > Neu differences was located at BAs 10, 11 and 47 (Fig. 5). The ANOVA on this ROI’s current densities revealed a significant effect of Biological Saliency ($F(1,19)=4.354$, $p<0.05$, $\eta^2_p=0.131$). Maximal current densities were elicited by salient distracters. Main effect of Eccentricity was not significant. Second, another ROI was defined for those voxels showing maximal Prox > Dist differential current densities. As shown in Fig. 5, this ROI was located in the posterior parietal cortex (PCC; BA31). ANOVAs on its current densities showed a main effect of Eccentricity ($F(2,58)=4.525$, $\eta^2_p=0.135$). Post-hoc tests showed differences between Prox and Dist conditions (Med vs Dist differences being marginally significant: $p=0.054$).

3.3.4. P3

Inferior temporal cortex, comprising middle and inferior temporal gyri (BA 20, 21 and 37) formed the relevant ROI (Fig. 5), which involved those voxels in which maximal Prox > Dist differential current densities were observed. Main effects of Eccentricity were confirmed by ANOVAs to be significant in this ROI ($F(2,58)=3.486$, $\eta^2_p=0.107$). Post-hoc analyses carried out through the Bonferroni procedure indicated that significant differences were produced between Prox and Dist conditions (Fig. 5). No effects of Biological Saliency nor the interaction between Eccentricity and Biological Saliency were observed ($p>0.05$).

3.4. Experimental effects on behavior

Error rate and RTs in the digit categorization task are shown in Table 2. Non-parametric contrasts were performed due to non-normality (see section on Data Analysis). First, the seven conditions (D0, Npprox, Sprox, Nmed, Smed, Ndist, Sdist) were submitted to a Friedman contrast. Differences between conditions were significant in the case of RTs ($\chi^2=18.629$, $p<0.01$), but not in the case of errors ($p>0.05$). Subsequently, pairwise contrasts on RTs were tested through the Wilcoxon method. On the one hand, and with the aim of testing whether distracters elicited a significant effect, D0 was compared with the average of the distracter conditions, differences being significant ($Z=-3.198$, $p<0.001$). On the other hand, each of the six conditions presenting distracters was compared to each other. No differences were observed with respect to Eccentricity (Npprox vs Nmed, Npprox vs Ndist, Nmed vs Ndist, Sprox vs Smed, Sprox vs Sdist, Smed vs Sdist) nor with respect to Biological Saliency (i.e., Npprox vs Sprox, Nmed vs Smed and Ndist vs Sdist) ($p>0.05$ in all cases).

In order to test the linkage between RTs and critical ERP components, a multiple regression analysis was carried out using the Enter method. RTs were the dependent variable, and predictor variables were N2olp, N2ft and P3 amplitudes at the scalp level (i.e., spatial factor scores). The regression model was shown to be significant (corrected $R^2=0.129$, $F(3,176)=9.809$, $p<0.001$). A strong association of RTs with N2olp and P3 was observed ($\beta=-0.211$ and $-0.368$, respectively, $p<0.005$ in both cases), but not with posterior N2ft ($\beta=0.009$, $p>0.05$). The positive association of RTs with Nolp (a negative component showing maximal amplitudes to peripheral—medial and distal-distracters) and their negative association with P3 (a positive component showing maximal amplitudes to central distracters) point to an influence of eccentricity processing on behavior, not detected in ANOVAs described above. Concretely, neural processes linked to central distracters caused longer RTs.

4. Discussion

The first scope of this study was to explore whether mechanisms underlying exogenous attention to peripheral distracters differ to some extent from those triggered by centrally presented distracters. In convergence with previous literature and as later explained, behavior (reaction times) showed the capability of central and peripheral distracters to capture exogenous attention, but was unable to provide strong discriminative information. Importantly, neural results clearly confirmed the central–peripheral segregation, as suggested both by temporal and spatial electrophysiological data. N2, an ERP component indexing exogenous attention (Carretié et al., 2004a; Daffner et al., 2000; Folstein & Van Petten, 2008; Kenemans et al., 1989; 1992; Pazó–Álvarez et al., 2003; Rozenkrants & Polich, 2008), reflected processes related to processing of peripheral distracters, as revealed by scalp amplitude and source analyses of both N2olp (peak at 217 ms), and N2ft (peak at 274 ms). Indeed, both N2olp amplitude increment and N2ft amplitude decrement observed in response to peripheral distracters appear to signal greater exogenous attention. Later, P3 showed enhanced activity in response to centrally presented distracters. Latency, amplitude and source analyses suggest that this component would be functionally associated with spatial interference between target and central distracters. In the next paragraphs, these results will be discussed step by step.

As indicated in the Results section, N2 was subdivided into two different components by principal component analyses. The first one, labeled here as N2olp, showed maximal amplitudes in response to peripheral distracters, particularly in occipital and lateral parietal scalp regions. Source localization analyses on the experimental N2olp effects observed in scalp indicated that peripheral distracters recruited the DAN to a greater extent than central distracters. This network is considered to be responsible for overt and covert reorienting of processing resources towards distracters according to their priority (Bisley & Goldberg, 2010; Gottlieb, 2007; Ptak, 2012). Interestingly, DAN areas involved in motor planning and execution are more clearly linked to exogenous than to endogenous attention, according to recent proposals (Smith & Schenk, 2012). For example, experimental prevention from planning or executing eye movements (Smith, Schenk, & Rorden, 2012) or lesions affecting normal oculomotor behavior (Gabay, Henik, & Gradstein, 2010) impair exogenous attention to distracters.

Specifically, and at least in the temporal window corresponding to N2olp, this activation was generated in supplementary motor area (SMA; medial/dorsal BA6), one of the frontal nodes of DAN (Kincaide, Abrams, Astafiev, Shulman, & Corbetta, 2005). The SMA plays an important role in the development of the intention–to–act and the specification and elaboration of action (Goldberg, 1985; Tanji, 1994). Importantly, SMA presents significant activity even in situations of covert attention (i.e., even when no motion—e.g., eye movement– is performed), as in the present case (Fairhall, Indovina, Driver, & Macaluso, 2009). The greater involvement of DAN areas in response to peripheral distracters is not a surprising result. As indicated in the introduction, non-foveal visual processing is mainly carried out by the magnocellular system. It conveys rudimentary visual information, poor in color and luminance...
details (i.e., only low spatial frequencies), but rapidly reaches “high-level” areas such as prefrontal and parietal cortices (Bar et al., 2006; Bullier, 2001). In fact, it has been recently shown the preferential involvement of magnocellular-type information in DAN to a greater extent than in VAN (i.e., the ventral attention network; Carretié, Ríos, Periáñez, Kessel, & Álvarez-Linera, 2012).

N2ft peak appeared 57 ms after N2olp peak. This second N2 component presented minimal amplitudes in response to trials containing peripheral distracters. This amplitude bias was mainly observed at midline parietal scalp regions. Source reconstruction showed lower activation of posterior cingulate cortex (PCC) in response to peripheral compared to central distracters. This pattern probably reflects attentional load in the digit categorization task. Indeed, an inverse correlation between the activity of PCC—one of the key nodes of the default mode network (e.g., Fransson & Marrelec, 2008; Greicius, Krasnow, Reiss, & Menon, 2003)—and attentional load has been reported. For instance, higher activity in PCC is seen under lower attentional load (Rauss, Pourtois, Vuilleumier, & Schwartz, 2012), and lower PCC activity is observed with higher sensory competition (Geng et al., 2006) and perceptual load (Xu, Monterosso, Kober, Balodis, & Potenza, 2011). Therefore, N2ft-associated PCC activity would indicate lesser perceptual/cognitive effort in the ongoing task in peripheral distracter conditions. As may be appreciated from data described above to this moment, present results suggest faster processing of distracters (mainly reflected in N2olp) than of targets (reflected in N2ft), in line with previous literature (Hickey, McDonald, and Theeuwes, 2006).

N2ft involved an additional source of experimental effects that informed on the second aim of this experiment, consisting of testing the effect of biological saliency of distracters. The main result at this respect was that biologically salient distracters elicited greater N2ft amplitudes regardless of their eccentricity. These results are convergent with previous studies indicating that the emotional content of stimulation is detected irrespective of its eccentricity with respect to fixation (Calvo et al., 2008; Rigoulot et al., 2011; 2012), and confirm that magnocellular information is sufficient to recognize objects (Thorpe et al., 2001) and to evaluate their associated relevance (Bar et al., 2006). Studies leaded by Rigoulot also recorded ERPs and, though experimental conditions were very different from current ones (e.g., stimuli consisted of facial expressions, eliciting the face-specific ERP topography, and no distracter vs relevant stimuli were employed), present data converge with them in that biological saliency modulation was reflected very early in ERPs (less than 300 ms from stimulus onset; see also Bayle et al., 2009). Importantly, even if attention was not explicitly directed towards the emotional content of stimuli, as in the present study, biological saliency modulation irrespective of eccentricity remained (Rigoulot et al., 2012). However, there is evidence of biological saliency/emotion neural insensitivity when stimulation appears over 8.21° from fixation (De Cesarei et al., 2009). These latter data, along with the fact that we observed the biological saliency effect at the neural but not at the behavioral level (this result will be discussed later), suggest that other factors can modulate this effect and that further research on this issue is needed.

The neural origin of this biological saliency effect was located in the polar/ventral prefrontal cortex (PFC). Enhanced activity in these regions while exogenous attention is directed to biologically salient stimulation has been previously reported (Carretié, Hinojosa, Mercado, & Tapia, 2005; Carretié, Hinojosa, Albert, & Mercado, 2006; Vuilleumier et al., 2001). This prefrontal area has neurons specializing in the identification of objects and faces (Tanibuchi & Goldman-Rakic, 2003). Several findings indicate that the ventral PFC receives inputs from early stages of the visual cortex (e.g., V2: see Bar, 2003; Bar et al., 2006), allowing this prefrontal area to rapidly extract and detect significant elements of the visual scene. Although this rapid visual information that reaches the ventral PFC is of magnocellular nature, it is sufficient for the development of rapid evaluation processes (Bar, 2003; Bar et al., 2006; Kveraga, Boshyan, & Bar, 2007). The fact that polar/ventral PFC activity is not dependent on the eccentricity of distracters reinforces the idea that it manages magnocellular information, which is present both in central and peripheral distracters (contrarily, parvocellular information is mainly managed in the case of centrally presented stimuli). Furthermore, it also supports the notion that this cortical area is in charge of evaluating biological saliency taking into account this imprecise information (Bar et al., 2006; Carretié, Albert, López-Martín, & Tapia, 2009a).

Finally, P3 showed greater amplitudes in response to central distracters. Source analyses revealed inferior temporal cortex (approximately TEO region) to be the origin of the experimental effects observed in this component. Enhanced activations in response to bilateral distracters presented at low eccentricities—as compared with those elicited by distracters presented at high eccentricities—have been previously reported in retinotopic cortices (Schwartz et al., 2005). As indicated in the introduction, spatial competition causes a complex “push–pull” or “biased competition” pattern of neural activity at extrastriate visual areas, mainly at V4 and TEO, aimed at suppressing or inhibit the processing of the distracter and to enhance the processing of the target (Beck & Kastner, 2005; Desimone, 1998; Kastner & Pinsk, 2004; Kastner & Ungerleider, 2000; Miller et al., 1993; Reynolds et al., 2000). Biased competition neutralizes the mutual suppression that typically affects responses to different stimuli presented in the same (large) receptive field of V4 and inferior temporal neurons, among other retinotopic areas. Thus, when top-down mechanisms prioritizes one of these stimuli as being task relevant -target- and the others become task irrelevant -distracters-, the neural response to the former is as strong as if presented alone (Chelazzi, Duncan, Miller, & Desimone, 1998; Desimone, 1998). The fact that increased responses towards targets concuring with central distracters was produced relatively late in time (on average P3 peaked at 386 ms from stimulus onset) supports the idea that this effect reflects top-down control from hierarchically superior structures of the brain, which may influence or bias the level of sensory processing of stimulation (see also Pessoa, Kastner, & Ungerleider, 2003).

Present results are a good example of the greatest sensitivity of ERPs to the effects of certain exogenous attention tasks as compared to behavioral responses (see also Holmes, Kiss, & Eimer, 2006). Reaction times showed the interfering effect of distracters, since they were longer when they were present than in the non-distracter condition. Additionally, regression analyses between behavior and ERP amplitudes indicated that neural processes triggered by central distracters caused longer reaction times than those triggered by peripheral distracters. However, ANOVAs did not detect significant direct effects of eccentricity on behavior. Indeed, previous literature is not consistent at this respect. Whereas some previous data suggest that exogenous attention is particularly efficient for peripheral distracters (i.e., they capture attention to a greater extent than central distracters: Chen & Treisman, 2008; Juola, Koshino, & Warner, 1995), others report exogenous attention biases towards central distracters (Beck & Lavie, 2005). This discrepancy may be explained by the variable processing demands associated with the specific ongoing cognitive task. In the present study, and as described above, both an advantage for peripheral and for central distracters was patent at the neural level (at different moments and neural sources). Taking into account (i) that behavior is the final single output of the complete set of neural processes (not always convergent), and (ii) that, from an evolutionary point of view, there should not exist a clear behavioral unbalance between exogenous attention captured by peripheral and central distracters since both situations may be relevant for survival, the absence of
clear behavioral advantages as a function of distracter eccentricity is not surprising. Additionally, present results suggest that, at least using the current experimental conditions, the complementary neural effects of low and high eccentricity contribute to a greater extent to behavioral performance than the neural effects of biological saliency.

Additional research is needed in order to evaluate how factors other than those explored here may modulate exogenous attention to peripheral and central distracters. One of them, particularly other than those explored here may modulate exogenous attention to peripheral and central distracters. One of them, particularly other than those explored here may modulate exogenous attention to peripheral and central distracters. One of them, particularly other than those explored here may modulate exogenous attention to peripheral and central distracters. One of them, particularly other than those explored here may modulate exogenous attention to peripheral and central distracters. One of them, particularly


