

Stimulus-Locked and Response-Locked ERP Correlates of Spatial Inhibition of Return (IOR) in Old Age

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Abstract. Behavioral research has shown that Inhibition of Return (IOR) is preserved in old age although at longer time intervals between cue and target, which has been interpreted as reflecting a later disengagement from the cue. A recent event-related potential (ERP) study attributed this age-related pattern to an enhanced processing of the cue. Previous ERP research in young samples indicates that target and response processing are also affected by IOR, which makes interesting to study the ERP correlates of IOR from cue presentation to response execution. In this regard, in the present study stimulus-locked (cue-locked and target-locked) and response-locked ERPs were explored in healthy young and older participants. The behavioral results indicated preserved IOR in the older participants. The cue-locked ERPs could suggest that the older participants processed the cue as a warning signal to prepare for the upcoming target stimulus. Under IOR, target-locked ERPs of both age groups showed lower N1 amplitudes suggesting a suppression/inhibition of cued targets. During the P3 rising period, in young subjects a negative shift (Nd effect) to cued targets was observed in the lower visual field (LVF), and a positive shift (Pd effect) in the upper visual field. However, in the older group the Nd effect was absent suggesting a reduction of attentional resolution in the LVF. The older group showed enhanced motor activation to prepare correct responses, although IOR effects on response-locked lateralized readiness potential LRP indicated reduced response preparation to cued targets in both age groups. In general, results suggest that the older adults inhibit or reduce the visual processing of targets appearing at cued locations, and the preparation to respond to them, but with the added cost of allocating more attentional resources onto the cue and of maintaining a more effortful processing during the sequence of stimuli within the trial.

Keywords: aging, spatial IOR, EEG, stimulus-locked ERP, response-locked ERP

When the focus of attention has been disengaged from the location of an uninformative cue, the time to respond to a target presented at that location is slower when the interval between the cue and the target is longer than approximately 250 ms (Posner & Cohen, 1984). This phenomenon, called Inhibition of Return (IOR) by Posner, Rafal, Choate, and Vaughan (1985) is considered an essential attention-shifting mechanism that helps in preventing the focus of attention to return to previously explored locations. Since its discovery, IOR has been observed in a wide variety of experimental situations within the visual, auditory, and tactile modalities (e.g., Spence, Lloyd, McGlone, Nichols, & Driver, 2000). IOR has also been observed across a variety of tasks, including detection, localization, and discrimination tasks (see Klein, 2000, for a review), and even in natural scenes (Klein & MacInnes, 1999), which has led to consider it as a basis for selecting important information. IOR has been classically studied with behavioral measures, and its neural correlates are still poorly understood although recent

research indicates that IOR may arise from a combination of inhibited perceptual processing (Gutiérrez-Domínguez et al., 2014; Handy, Jha, & Mangun, 1999; McDonald, Ward, & Kiehl, 1999; Prime, Visser, & Ward, 2006; Prime & Ward, 2004, 2006), a more conservative response criterion on cued trials relative to uncued trials (Ivanoff & Klein, 2001, 2006), and an inhibition of motor (Amenedo, Gutiérrez-Domínguez, Mateos-Ruger, & Pazo-Álvarez, 2013; Pastötter, Hanslmayr, & Bäuml, 2008) and oculomotor (Ro, Farnè, & Cahng, 2003; Ro, Pratt, & Rafal, 2000) programming. In fact, the evidence supporting several mechanisms agrees with the proposal that IOR may arise from multiple processes (Kingstone & Pratt, 1999; Taylor & Klein, 1998, 2000).

Behavioral studies in the context of aging research have found that IOR is essentially preserved in old age (Faust & Balota, 1997; Hartley & Kieley, 1995; McCrae & Abrams, 2001; Poliakoff, Coward, Lowe, & O'Boyle, 2007) although at longer time intervals between cue and target

presentations (Castel, Chasteen, Scialfa, & Pratt, 2003; Langley, Fuentes, Hochhalter, Brandt, & Overmier, 2001; Langley, Fuentes, Vivas, & Saville, 2007; Langley, Vivas, Fuentes, & Bagne, 2005; Wascher, Falkenstein, & Wild-Wall, 2011). This longer time course of IOR in old age has been recently interpreted as reflecting a later disengagement from the cue location in aged persons (Castel et al., 2003; Langley, Friesen, Saville, & Ciernia, 2011).

In a typical IOR task, each trial is composed of a sequence of stimuli beginning with the presentation of an uninformative spatial cue followed by a target that can appear at the same or different location with cue-to-target onset asynchronies (CTOAs) longer than 250–300 ms. In this context, the subject is required to give a button press to the target and to ignore the previous cue. During the period between the onset of the cue and the emission of a correct response to the target, several processes related to both attention and motor mechanisms take place. Specifically, and following task instructions, the essential processes contributing to the recorded RT are the inhibition or reduction of the processing of the cue, the focusing of attention onto the target, and the selection and preparation of the correct motor command. In visual search and in choice reaction tasks the ERP correlates of target and response processing have been found affected by age (see, e.g., Amenedo, Lorenzo-López, & Pazo-Alvarez, 2012; Falkenstein, Yordanova, & Kolev, 2006).

Traditionally, the research on the neurocognitive correlates of IOR has focused on the processing of the target stimulus (see Gutiérrez-Domínguez et al., 2014). ERP studies in young adults have shown that spatial IOR is associated with amplitude modulations in several target-locked ERP components. However, the direction of such modulations has not always been the same, since several studies have found amplitude reductions while other have observed amplitude increases. Visual P1 and N1 components have been the most studied in this context. Regarding P1, amplitude reductions have been observed (Chica & Lupiáñez, 2009; McDonald et al., 1999; Prime & Jolicoeur, 2009; Prime & Ward, 2004; Prime et al., 2006; Tian, Klein, Satel, Xu, & Yao, 2011; Tian & Yao, 2008; Van der Lubbe, Vogel, & Postma, 2005; Wascher & Tipper, 2004) and generally interpreted as an early inhibition of the processing of previously cued target stimuli in visual areas. However, other studies failed to find P1 amplitude changes under IOR (Gutiérrez-Domínguez et al., 2014; Hopfinger & Mangun, 2001; Satel, Wang, Hilchey, & Klein, 2012), which has lead to a lack of consensus on the possible causal role of P1 in IOR (Satel et al., 2012). Regarding N1 component, the results are also divergent although when reviewing the literature a task characteristic shows up that may explain these discrepancies. Studies that have employed detection tasks have not found N1 amplitude modulations associated with IOR (Hopfinger & Mangun, 2001; van der Lubbe et al., 2005; Wascher & Tipper, 2004) while those that have employed a discrimination task have found N1 amplitude reductions (Gutiérrez-Domínguez et al., 2014; Prime & Jolicoeur, 2009; Prime & Ward, 2004, 2006). These findings are in agreement with the well-established functional role of N1 in visual discrimination

processes (van der Lubbe et al., 2005; Vogel & Luck, 2000). Besides P1 and N1, other IOR-related effects have been reported on target-locked ERPs. These effects resulted from amplitude changes in the ERP waveforms falling within latency intervals that did not coincide specifically with the peak of any component (Eimer, 1994; Gutiérrez-Domínguez et al., 2014; McDonald et al., 1999; Prime & Jolicoeur, 2009; Prime & Ward, 2004, 2006; Prime et al., 2006; Tian, Chica, Xu, & Yao, 2011; Wascher & Tipper, 2004). Among these effects, two of them have been the most frequently observed, and consisted of a negative shift (generally called in this context of research *Negative difference*, or Nd) or a positive shift (*Positive difference*, or Pd) occurring during the rising period of the P3 component. The interpretation of such shifts is still under debate (Gutiérrez-Domínguez et al., 2014; Hopf et al., 2000, 2004; McDonald, Hickey, Green, & Whitman, 2009; Tian, Chica, et al., 2011). The age-related changes of above target-locked IOR effects have not been previously studied.

However, the described IOR effects on target-locked ERP in young adults have not always been associated with behavioral IOR effects (i.e., slower RTs to cued targets), suggesting that possibly response-related processing is also influenced (Pastötter et al., 2008). In this sense, studies exploring lateralized readiness potentials (LRP) have suggested that motor processes per se are not affected by IOR (Prime & Ward, 2004, 2006; Prime et al., 2006) although this interpretation has been recently questioned employing time-frequency analyses of EEG activity (Amenedo et al., 2013; Pastötter et al., 2008), and suggesting that spatial IOR is associated with sensorimotor idling (Amenedo et al., 2013) and with motor inhibition (Amenedo et al., 2013; Pastötter et al., 2008) when responding to previously cued targets. Moreover, the results of its age-related changes suggest that aging affects the pattern of cortical oscillations during response preparation and execution, but that spatial IOR effects on sensorimotor activity are generally preserved (Amenedo et al., 2013).

Regarding the processing of the cue, the only study having explored its ERP correlates, and focusing on the analysis of frontocentral N2 component, has found that IOR effects are associated with large amplitudes in young subjects (Wascher et al., 2011) that have been interpreted as reflecting inhibition of cue processing. Moreover, this study, to our knowledge, is the only study that has explored the age-related changes associated with the cue processing. The authors found an absence of the frontocentral N2 observed in young participants that was interpreted as a processing of the cue as if it was a relevant stimulus (Wascher et al., 2011).

In this context, the analysis of stimulus and response-related EEG activity from cue presentation to response execution could give interesting and complementary information on the mechanisms underlying IOR, and their age-related changes. In this regard, the main objective of the present study was to explore the age-related effects on time-amplitude changes (ERP) in the EEG activity related to both stimulus and response processing under spatial IOR during the execution of a cue-back task. In this task,

the stimuli were presented along the vertical axis to prevent possible interactions between IOR and stimulus-response spatial compatibility effects (see Ivanoff, Klein, & Lupiañez, 2002 for a review). Due to the well established visual asymmetries when the stimuli are presented along the vertical meridian (Karim & Kojima, 2010; Rezec & Dobkins, 2004; Thomas & Elias, 2011), and to the existence of previous results showing that these visual asymmetries also affect IOR (Gutiérrez-Domínguez et al., 2014), the data from each visual field were analyzed separately. As IOR onset is delayed in older adults, to ensure the elicitation of reliable IOR effects in these participants, a cue-to-target onset asynchrony (CTOA) of 2,000 ms, which has previously been found to activate IOR in young and older adults, was employed (Castel et al., 2003; Langley et al., 2007). With this design, to explore stimulus processing in the EEG activity, the ERPs to the cue (cue-locked ERPs) and to the target (target-locked ERPs) were analyzed. To explore response processing, the ERPs to correct response execution (response-locked ERPs, LRP) were examined.

Methods

Participants

Ten young (8 females, 24.5 ± 5.79 years, range 19–37) and 10 older adults (8 females, 67.2 ± 5.65 years, range 61–78) participated in the study. All participants were healthy well-functioning without a history of neurological or psychiatric disorders, had normal or corrected-to-normal visual acuity, reported normal color vision, were right handed (Oldfield, 1971), and they were living by their own. The older participants obtained normal MMSE scores (28.1 ± 1.8 , range 26–30). Informed consent was obtained from all participants, and they obtained a monetary compensation for their participation.

Stimuli and Experimental Design

During the task (see Figure 1), one central and two peripheral (external edge 4.5° of visual angle from the center of the screen) light grey boxes (RGB 200,200,200, $1.5^\circ \times 1.5^\circ$ of visual angle) were always present in the vertical meridian of a computer screen (100 Hz resolution). A central fixation cross (RGB 150,150,150, $0.1^\circ \times 0.1^\circ$ of visual angle) was also present and participants were instructed to maintain fixation on it during the task performance. Each trial began with a 1,500 ms blank screen (RGB 50,50,50, average luminance 2.4 cd/m^2) that defined the background screen. After this, a blue (RGB 0,0,255, average luminance 8.3 cd/m^2) or red (RGB 175,0,0, average luminance 8.2 cd/m^2) patch was presented during 100 ms filling one of the two peripheral boxes (0.5 probability). This patch served as a cue for location or color dimension, and it was uninformative related to both location and color dimensions of the target. After a new blank

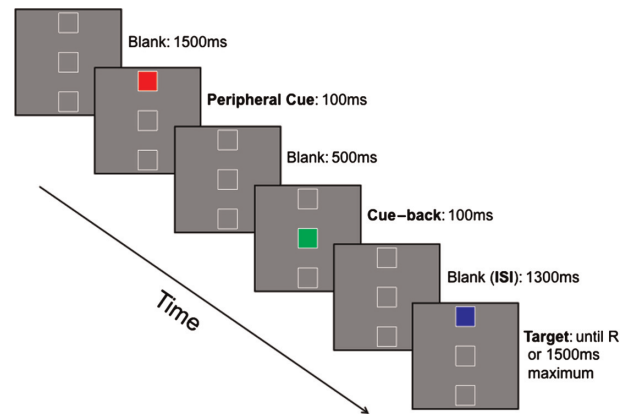


Figure 1. Characteristics of stimulus types and time sequence in the task.

screen of 500 ms duration, a cue-back consisting of a green patch (RGB 0,95,0, average luminance 8.4 cd/m^2) filling the central box was presented for 100 ms. After another blank interval of 1,300 ms, a target was presented until response execution or a maximum of 1,500 ms. Target stimuli consisted of a blue or red patch (0.5 probability), identical to the cue, filling the lower or upper box (0.5 probability). Target shared color or location with the cue in 50% of trials. The duration of the interval between the cue onset and the target onset (1,300 ms) defined a CTOA of 2,000 ms. Combining cue and target color and location, we obtained four design conditions: trials with both location and color cued; location cued, but not color; color cued, but not location; and neither location nor color cued. Participants were sitting in an armchair placed at 112 cm distance from the computer screen; they were asked to respond to target color (red or blue) irrespective of its location by pressing a button (Response Box RB-834 model, Cedrus Corporation) with their right hand to one color and another button with their left hand to the other color. Assignment of response hand to each color was counterbalanced across participants. Both speed and accuracy were stressed in the instructions. The task was divided in 25 blocks of 64 trials, mixing different trial conditions in each block randomly. There was a 3 s rest between each block that participants could interrupt to continue with the task as soon as they wanted by pressing a button of the response device. In this paper we focus our analyses on the comparison between uncued trials and location cued trials.

Recording and Analysis

Behavioral Data

Reaction times (RTs) and accuracy (hits and errors) were on-line recorded for all participants to all conditions in all experimental blocks. Only RT values associated with correct responses were considered for data analyses. Responses were considered correct when RTs were within ± 3 standard deviations of the mean RT for each

condition in each age group. Mean correct RTs and error rates (%) in each visual field were submitted to separate mixed-model analyses of variance (ANOVAs) with age group (young vs. older) as the between-subjects factor, and spatial cueing (uncued vs. cued) as the within-subject factor. Whenever appropriate, degrees of freedom were corrected by the conservative Greenhouse-Geisser estimate. An alpha level of .05 was used for all analyses.

Electroencephalographic (EEG) Recording

Recordings were made in an electrical shielded and sound attenuated room. Continuous EEG activity was recorded with a Brain Vision Recorder (Brain Products, Inc., Gilching, Germany) from 60 scalp Ag-AgCl electrodes placed according to the extended 10/20 International System. The cephalic electrodes were referred to the nose tip and grounded with an electrode placed at 10% of the nasion-inion distance above nasion. Vertical and horizontal electrooculogram (EOG) were recorded from above and below the participant's left eye and from the outer canthi of both eyes, respectively. Electrode impedances were kept below 10 k Ω . Sampling rate was 500 Hz/channel. EEG signal was continuously amplified (10 K) and filtered online with a band pass of 0.01–100 Hz.

EEG Data Analysis

Data from all conditions were epoched into segments of 4,500 ms (–1,000 to 3,500 ms relative to cue presentation) and merged together for each participant. Artifacts were removed using EEGLAB v9.0.4.4b (Delorme & Makeig, 2004), a freely available open source software toolbox (Swartz Center for Computational Neurosciences, La Jolla, CA; www.sccn.ucsd.edu/eeqlab) running under Matlab R2011a (MathWorks, Inc., Natick, MA). The following procedure was used: First, epochs containing non-stereotyped artifacts (e.g., cable movement, swallowing) were manually removed, whereas epochs containing repeatedly occurring, stereotyped artifacts (e.g., eye blinks, muscle artifact, etc.) were kept. Then, extended *infomax* independent component analysis (ICA; Lee, Girolami, & Sejnowski, 1999; Bell & Sejnowski, 1995) was applied individually for each participant, using a weight change of $< 10^{-7}$ or 512 iterations as a stop criterion. Component activations were subsequently assessed and categorized as brain activity or non-brain artifact (e.g., muscle, electrode artifact, or eye movement activity) by visual inspection based on their scalp topographies, time courses, ERP images, and activation spectra. After identification of components constituting artifacts, individual EEG data containing all conditions were reconstructed without those components. Finally, epochs corresponding to each experimental condition were extracted from ICA-pruned data for each participant. The ICA-corrected segments of 4,500 ms (–1,000 to 3,500 ms relative to cue presentation) were used to obtain the cue-locked ERP waveforms for all conditions. Moreover, ICA-corrected data for all conditions were subsequently segmented into epochs of 2,000 ms (–500

to 1,500 ms relative to target presentation) to obtain target-locked ERPs, and of 2,500 ms (–1,500 to 1,000 ms relative to button press) to obtain response-locked ERPs (Vision Analyzer, version 2.0, Brain Products, Inc.).

Time-Amplitude Data Analysis

Two stimulus-locked (cue-locked and target-locked), and one response-locked ERP waveforms were obtained for each condition, visual field and participant separately. The cue-locked ERPs were computed by averaging the EEG segments relative to cue presentation (–1,000 to 3,500 ms). The target-locked ERPs were obtained by averaging the EEG segments relative to target presentation (–500 to 1,500 ms), and the response-locked ERPs were obtained by averaging the EEG epochs relative to correct button presses (–1,500 to 1,000 ms). Moreover, from these response-locked ERPs, the LRP was calculated across all lateralized electrodes according to the formula $[(LH \text{ electrode (right hand)} - (RH \text{ electrode (left hand)} + (RH \text{ electrode (left hand)} - (LH \text{ electrode (right hand)}))/2]$ were LH corresponds to left hemisphere, and RH to right hemisphere (Vision Analyzer, version 2.0, Brain Products, Inc.). To use a blind method for selecting the time intervals and the corresponding electrode sites with significant differences between age groups and cueing conditions, the stimulus-locked (cue-locked and target locked) and response-locked (LRP) ERP waveforms across all electrodes (the 60 electrodes for cue-locked and target-locked ERPs, and the lateralized electrodes for the LRP), and along the entire epoch for each participant, visual field, and condition were submitted to separate spatiotemporal analyses with BESA Statistics Software (v1.0, May 2012; BESA GmbH, Inc., http://www.besa.de/products/besa_statistics/). On these data, to calculate the time intervals and the electrodes with significant amplitude differences between age groups within each condition, and between conditions within each age group, an initial *t*-test (unpaired *t* for age group comparisons, and paired *t* for cueing condition comparisons; alpha level 0.05) were computed per data-point, electrode, and participant in each visual field separately. The resulting time-windows and electrodes with significant differences in amplitudes between age groups in each condition, and between uncued and cued conditions in each age group, were subsequently passed onto a cluster-based permutation testing for each visual field separately with correction for multiple comparisons. In this procedure, clustering in time (across time points) and space (across electrodes) is based on the results of the preliminary *t*-test. Depending on the cluster-alpha setting, adjacent data points are subsumed to form a cluster. The significance of these data clusters is probed during permutation testing. The main idea behind this permutation test is that if a statistical effect is found over an extended time period in several neighboring channels, it is unlikely that this effect occurred by chance. For the present analyses, 1,000 permutations with a 4 cm distance between neighbor electrodes, and with an initial alpha level of 0.05, were executed. Finally, the mean amplitude values of the time intervals where permutations

showed significant differences were calculated for the corresponding electrodes and subsequently submitted to parametric statistical testing by means of analyses of variance (ANOVAs) as follows. Specifically, to parametrically check for possible effects of age or the possible interactions between age and electrode, and/or cueing condition, the mean amplitude data corresponding to each latency interval and the cluster of electrodes were submitted to mixed-model ANOVAs with age group as the between-subjects factor, and electrode and cueing condition as the within-subjects factors where appropriate (the cueing condition was not considered as a factor in the ANOVAs of the cue-locked ERPs because it has no sense to check for possible IOR effects when examining stimulus-locked ERPs before target presentation). When the effects of age, cueing condition or the interaction between age group and cueing condition were significant, separate repeated-measures ANOVAs with electrode and cueing condition as within-subject factors were performed for each age group separately. Whenever appropriate, degrees of freedom were corrected by the conservative Greenhouse-Geisser estimate. When necessary, Bonferroni correction for multiple comparisons was used. The level of significance was established in alpha 0.05 for all analyses.

Results

Behavioral Data

The ANOVAs performed on behavioral data showed a main effect of age group on RT values in both visual fields (upper visual field, UVF: $F(1, 18) = 8.77$, $p < .01$, $\eta^2 = .33$; lower visual field, LVF: $F(1, 18) = 8.84$, $p < .01$, $\eta^2 = .33$) that was due to slower RTs in the older participants in all conditions (see Table 1). Cueing condition also had significant effects on RT values, which were slower for cued targets in both age groups (UVF: $F(1, 18) = 25.54$, $p < .0001$, $\eta^2 = .59$; LVF: $F(1, 18) = 8.9$, $p < .01$, $\eta^2 = .33$).¹ A significant interaction between age group and spatial cueing was observed on the RTs in the UVF ($F(1, 18) = 7.37$, $p < .02$, $\eta^2 = .29$) but not in the LVF ($F(1, 18) = 2.28$, $p = .15$, $\eta^2 = .11$). Separate repeated measures ANOVAs for each age group with spatial cueing (uncued vs. cued) as within-subject factor showed significant effects of IOR in both age groups although of higher magnitude in the older participants in the UVF (young: $F(1, 9) = 12.05$, $p < .01$, $\eta^2 = .57$; older:

$F(1, 9) = 17.02$, $p < .01$, $\eta^2 = .65$; see Table 1), but not in the LVF (young: $F(1, 9) = 7.8$, $p < .05$, $\eta^2 = .46$; older: $F(1, 9) = 7.05$, $p < .05$, $\eta^2 = .44$). No effects of age group were found on the error rates, which were similar in young and older adults (UVF: $F(1, 18) = .78$, $p = .4$, $\eta^2 = .04$; LVF: $F(1, 18) = 1.52$, $p = .23$, $\eta^2 = .08$) and in both cueing conditions (UVF: $F(1, 18) = 4.06$, $p = .06$, $\eta^2 = .18$; LVF: $F(1, 18) = .12$, $p < .73$, $\eta^2 = .01$). No interactions between age group and spatial cueing (UVF: $F(1, 18) = .23$, $p = .64$, $\eta^2 = .01$; LVF: $F(1, 18) = 2.23$, $p < .15$, $\eta^2 = .11$) were observed on error rates (see Table 1).

In general, the above results indicated that, with similar error rates in both age groups and cueing conditions, the behavioral effects of IOR were preserved in the older participants. Moreover, the results indicated higher IOR effects on response times of the older participants to targets presented in the UVF.

ERP Data

Cue-Locked ERPs

In general, the cue-locked ERPs were more negative in the older than in the young participants in both visual fields and cueing conditions from cue presentation to target offset (see Figure 2). The results of the cluster-based permutation analyses showed significant differences in several time intervals and clusters of electrodes in both visual fields and conditions after cue presentation as specified in Table 2 and Figure 2. The mean amplitude values in each of these time intervals and the corresponding electrodes within each cluster were entered into separate mixed-model ANOVAs for each visual field with age group (young vs. older) as between-subjects factor, and electrode (those indicated in Table 2 for each time interval) as within-subject factor. The results of these ANOVAs, and the mean amplitude values for the electrode with maximum age-related difference in each time interval and cluster are shown in Table 3. These analyses confirmed the existence of more negative mean amplitudes in the older participants across visual fields and cueing conditions. Specifically, the age-related differences in amplitude in both cueing conditions and visual fields were generally maximal at centro-parietal and parieto-occipital electrodes, and within time intervals corresponding to cue, cue-back, and target processing (see Figure 2 and Table 3).

¹ Limitations to using RT to assess age-related differences in cognitive processes have motivated the development of several RT data transformations to take into account the contribution of the response slowing generally observed in aged samples. One such transformation divides individual's condition RT's or condition difference scores by their baseline RTs. As a result, these proportionally transformed scores identify task-specific group differences that are independent of baseline RT differences, and they allow within-group comparisons of performance across conditions with different baseline RTs. Such transformed scores have proved instrumental in IOR studies for comparing cueing effects across age groups (Faust & Balota, 1997; Langley et al., 2001). Therefore, and following the suggestion of one anonymous reviewer, we used the procedure employed by Langley et al. (2001). In this procedure, the percentage of slowing in the cued condition relative to the baseline RT (uncued condition) is calculated in each participant by using the formula: $(\text{Cued RT} - \text{Uncued RT}) / \text{Uncued RT} \times 100$. Once applied the above formula, a one-sample *t*-test is performed in each age group and condition separately to test whether the new transformed IOR scores are significantly different from zero (alpha level 0.05). The results of the above transformation and analyses on the present data showed that the IOR effects remained significant in both age groups and visual fields (young: UVF: $t = 3.29$, $p < .01$; LVF: $t = 2.22$, $p < .05$; older: UVF: $t = 4.55$, $p < .001$; LVF: $t = 2.94$, $p < .02$).

Table 1. Mean RT (ms) and error rate (%) in each age group across visual fields and cueing conditions

	Young				Older			
	Cued	Uncued	Cued-Uncued	Transformed IOR score*	Cued	Uncued	Cued-Uncued	Transformed IOR score*
UVF	540.15	528.94	11.21	2.3	720.91	683.66	37.24	5.29
RT	(132.94)	(133.61)	(10.21)	(2.15)	(128.41)	(112.29)	(28.55)	(3.67)
Error	2.10	1.30	0.80		3.40	2.10	1.30	
	(1.45)	(1.34)	(1.55)		(4.65)	(2.85)	(2.91)	
LVF	536.34	527.77	8.57	1.85	715.84	689.68	26.15	3.75
RT	(132.37)	(134.60)	(19.59)	(4.46)	(130.11)	(118.53)	(31.15)	(4.03)
Error	1.80 (1.13)	2.30 (2.11)	-0.50 (2.01)		3.80 (3.22)	3.00 (3.40)	0.80 (1.87)	

Note. *(Cued RT – Uncued RT)/Uncued RT × 100.

Target-Locked ERPs

Between-Group Analyses: Age Effects

The separate permutation analyses for each visual field on the target-locked ERPs comparing age groups within each cueing condition showed in general the existence of lower amplitudes in the older group as shown in Table 4 and in Figure 3.

Mean amplitudes were calculated for each of the time intervals and electrodes included in the corresponding cluster in all subjects, visual field and cueing condition (see Table 4). In order to check the existence of possible interactions between age group and cueing condition, or between age group and electrode, separate mixed-model ANOVAs for each visual field were run on these mean amplitudes with age group (young vs. older) as the between-subjects factor, and cueing condition (cued vs. uncued) and electrode (those electrodes that were common for cued and uncued conditions in the cluster corresponding to each time interval as shown in Table 4 and in Figure 3) as the within-subject factors. The results of these analyses were as follows.

In the UVF, the results confirmed a significant effect of age group ($F(1, 18) = 6.08, p < .03, \eta^2 = .25$) with lower mean amplitudes in the older group (estimated means, young: $7.38 \pm 1.33 \mu\text{V}$; older: $2.74 \pm 1.33 \mu\text{V}$). Moreover, significant cueing effects were observed ($F(1, 18) = 36.82, p < .0001, \eta^2 = .67$) indicating more positive amplitudes in the cued condition in both age groups (estimated means, cued: $5.12 \pm .94 \mu\text{V}$; uncued: $5.0 \pm .93 \mu\text{V}$). No interaction between age group and cueing condition was observed ($F(1, 18) = 2.81, p = .11, \eta^2 = .13$). Significant effects of electrode ($F(42, 756) = 8.5, p < .0001, \eta^2 = .32$) and an interaction between electrode and age group ($F(42, 756) = 3.04, p < .001, \eta^2 = .15$) indicated the existence of maximum positive amplitudes at posterior electrodes in the young group while a more homogeneous distribution was observed in the older group (see voltage and statistic maps in Figure 3).

In the LVF similar results were observed, with main effects of age group ($F(1, 18) = 6.95, p < .02, \eta^2 = .28$; estimated means, young: $7.4 \pm 1.62 \mu\text{V}$; older: $.99 \pm 1.62 \mu\text{V}$) and cueing condition ($F(1, 18) = 6.21, p < .03, \eta^2 = .26$; estimated means, cued: $4.05 \pm 1.15 \mu\text{V}$; uncued: $3.98 \pm 1.14 \mu\text{V}$) with no interaction between age group and cueing ($F(1, 18) = .06, p = .82, \eta^2 = .003$). Again significant effects of electrode ($F(32, 576) = 11.35, p < .0001, \eta^2 = .39$) and an interaction between electrode and age group ($F(32, 576) = 6.51, p < .001, \eta^2 = .27$) indicated maximum positive amplitudes at posterior electrodes in the young group and a more homogeneous distribution in the older group (see voltage and statistic maps in Figure 3).

In general, the age-related effects on target-locked ERPs were similar in both visual fields and showed a change in amplitude distribution within the latency range of P3. Specifically, while the young subjects showed the typical posterior maximum amplitudes, the older participants showed a more widespread distribution that included both anterior and posterior electrode sites.

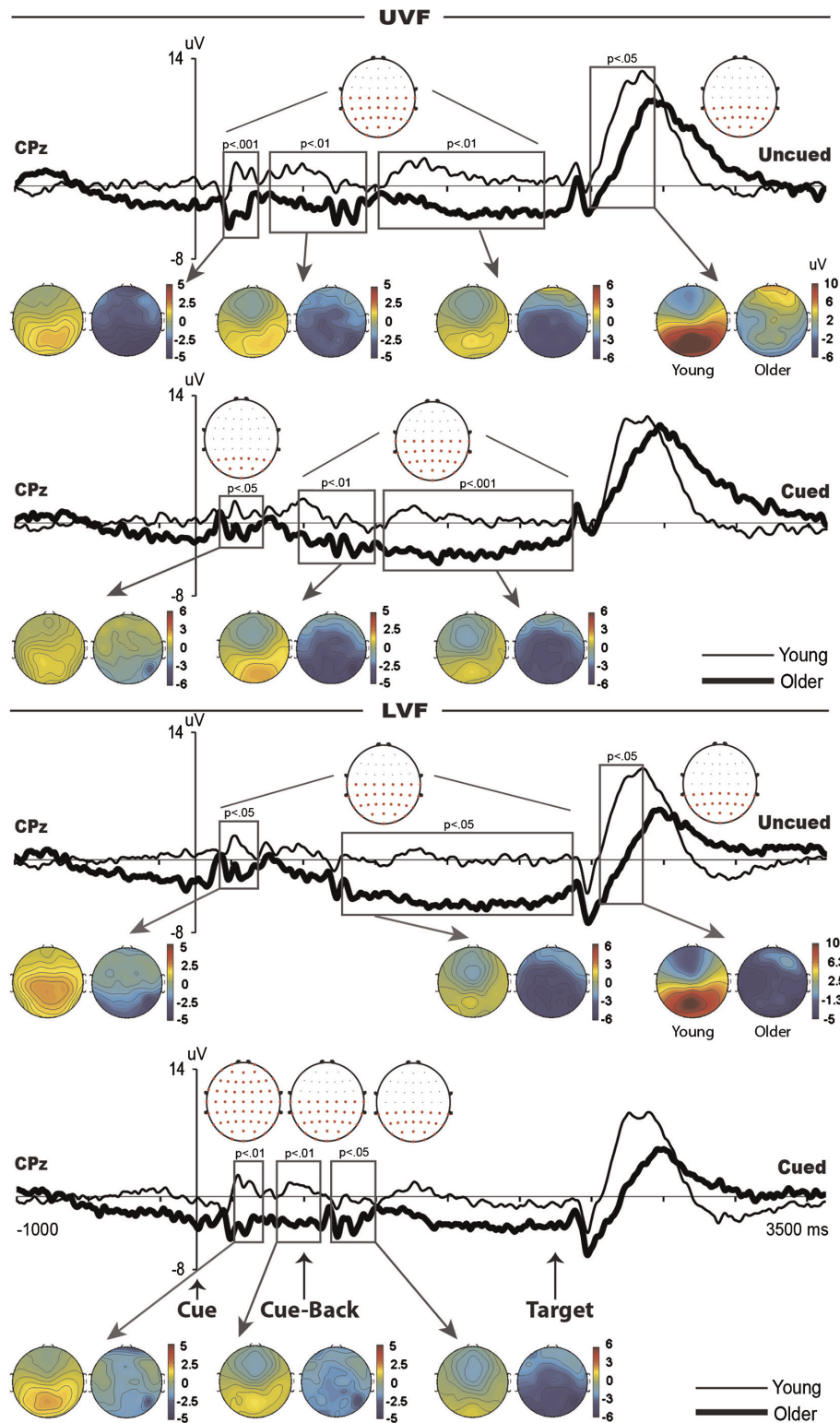


Figure 2. Cue-locked ERP waveforms superimposed for each age group across visual fields and cueing conditions, and the corresponding voltage maps. Grey rectangles indicate the time intervals where significant differences were found by permutation analyses. Maps with red dots indicate the electrode sites where significant differences were observed in those time intervals.

Table 2. Cue-locked ERPs. Between-subjects analyses: Age effects. Time intervals and the corresponding electrode clusters where permutation analyses showed significant differences between age groups. Results are shown for each visual field and cueing condition

	Uncued		Cued	
	Time interval (ms)	Electrode cluster	Time interval (ms)	Electrode cluster
UVF	190–320*	T7,C5,C3,C1,Cz,C2,C4,C6,T8,	160–280 ⁺	P7,P5,P3,P1,Pz,P2,P4,P6,P8,PO7,
	420–930 [#]	TP7,CP5,CP3, CP1,CPz,CP2,CP4,		PO3,POz,PO4,PO8,O1,Oz,O2
	1050–2100 [#]	CP6,TP8,P7,P5,P3,P1,Pz,P2,P4,P6,		
		P8,PO7,PO3,POz,PO4,PO8,O1,Oz,O2		
	2,200–2,500 ⁺	TP7,CP5,CP3,CP1,CPz,CP2,CP4,	520–950 [#]	T7,C5,C3,C1,Cz,C2,C4,C6,T8,TP7,
		CP6,TP8,P7,P5,P3,P1,Pz,P2,P4,P6,	1,000–2,100*	CP5,CP3,CP1,CPz,CP2,CP4,CP6,TP8,
		P8,PO7,PO3,POz,PO4,PO8,O1,Oz,O2		P7,P5,P3,P1,Pz,P2,P4,P6,P8,PO7,PO3,
				POz,PO4,PO8,O1,Oz,O2
LVF	180–250 ⁺	T7,C5,C3,C1,Cz,C2,C4,C6,T8,TP7,	220–330 [#]	Fp1,Fp2,AF7,AF3,AFz,AF4,AF8,F7,F5,
	750–2150 ⁺	CP5,CP3,CP1,CPz,CP2,CP4,CP6,		F3,F1,Fz,F2,F4,F6,F8,FT7,FC5,FC3,
		TP8,P7,P5,P3,P1,Pz,P2,P4,P6,P8,PO7,		FC1,FCz,FC2,FC4,FC6,FT8,T7,C5,
		PO3,POz,PO4,PO8,O1,Oz,O2		C3,C1,Cz,C2,C4,C6,T8,TP7,CP5,CP3,
				CP1,CPz,CP2,CP4,CP6,TP8,P7,P5,P3,
				P1,Pz,P2,P4,P6,P8,PO7,PO3,POz,PO4
				PO8,O1,Oz,O2
	2220–2540 ⁺	TP7,CP5,CP3,CP1,CPz,CP2,CP4,	430–720 [#]	T7,C5,C3,C1,Cz,C2,C4,C6,T8,TP7,CP5,
		CP6,TP8, P7,P5,P3,P1,Pz,P2,P4,P6,		CP3, CP1,CPz,CP2,CP4,CP6,TP8,P7,P5,
		P8,PO7,PO3, POz,PO4,PO8,O1,Oz,O2		P3,P1,Pz,P2,P4,P6,P8,PO7,PO3,POz,
				PO4,PO8,O1,Oz,O2
			750–950 ⁺	TP7,CP5,CP3,CP1,CPz,CP2,CP4,CP6,
				TP8,P7,P5,P3,P1,Pz,P2,P4,P6,P8,PO7,
				PO3,POz,PO4,PO8,O1,Oz,O2

Notes. * $p < .001$, [#] $p < .01$, ⁺ $p < .05$.

Within-Group Analyses: Cueing Effects

Given that target-locked ERPs revealed different spatio-temporal patterns of electrode effects in each age group, differences between cued and uncued conditions were further examined in young and older participants separately by non-parametric analyses with BESA Statistics Software (v1.0, May 2012; BESA GmbH, Inc., Gräfelfing, Germany, http://www.besa.de/products/besa_statistics/) comparing data between cued and uncued conditions within each age group and visual field separately. This new analysis was performed in the entire target-locked ERPs waveforms and across all 60 electrodes to determine the time intervals and the electrode clusters with significant amplitude differences due to spatial cueing in each age group. The results of these permutation analyses are shown in Table 5 and Figure 4.

Young Participants

In the UVF, cluster-based permutations showed that the differences between cueing conditions in this age group (Table 5 and Figure 4) were due to lower amplitudes in the latency range of the N1 component (150–180 ms) in the cued condition, and to a positive shift during the rising period of P3 to cued target stimuli that will be thereafter referred as Pd effect (340–360 ms).

In the LVF significant differences were again observed within the N1 latency range (150–200 ms) showing lower N1 amplitudes to cued targets. In the P3 rising period significant differences were also found between cueing conditions although in this visual field the differences were within an earlier time interval (250–300 ms), and consisting of a negative shift to cued targets at more posterior electrodes than in the UVF (see Table 5 and Figure 4) that will be thereafter called Nd effect (250–300 ms).

The mean amplitudes of each of the above time intervals were calculated in each electrode of the corresponding cluster and submitted to repeated measures ANOVAs with cueing condition (cued vs. uncued) and electrode (the electrodes included in the corresponding cluster) as the within-subject factors for each visual field separately.

In the data of the UVF, the latency range of N1 (150–180 ms) showed significant effects of cueing condition ($F(1, 9) = 3.45$, $p < .05$, $\eta^2 = .28$) and electrode ($F(10, 90) = 2.83$, $p < .01$, $\eta^2 = .24$; maximum amplitude, FCz: $-2.95 \pm 1.2 \mu\text{V}$) with no interaction between them ($F(10, 90) = 1.11$, $p = .4$, $\eta^2 = .11$) that indicated lower mean amplitudes of N1 to cued targets (estimated means, cued: $-1.86 \pm .86 \mu\text{V}$; uncued: $-2.61 \pm .72 \mu\text{V}$). Within the latency range of the Pd effect (340–360 ms), the ANOVA showed significant effects of cueing condition ($F(1, 9) = 3.97$, $p < .05$, $\eta^2 = .31$) and electrode ($F(11, 99) = 7.35$, $p < .0001$, $\eta^2 = .45$; maximum

Table 3. Cue-locked ERPs: Between-subjects analyses: Age effects. Mean amplitudes (μV) are shown across visual fields and cueing conditions for latency intervals and the electrode where permutations showed maximum differences between age groups (standard deviation in parenthesis). F values for “age group” (1), “electrode” (2), and “age group by electrode” interaction (3). Significance levels and effect sizes are also shown

	Uncued	Cued
UVF	190–320 ms, P2 Young: 1.78 (2.02); Older: -2.80 (1.72) (1) $F(1, 18) = 20.71^{***}$, $\eta^2 = .53$ (2) $F(34, 612) = 1.3$ ns, $\eta^2 = .07$ (3) $F(34, 612) = 3.67^{***}$, $\eta^2 = .18$	160–280 ms, P6 Young: 0.78 (1.89); Older: -1.80 (1.76) (1) $F(1, 18) = 5.61^*$, $\eta^2 = .24$ (2) $F(16, 288) = 1.5$ ns, $\eta^2 = .07$ (3) $F(16, 288) = 0.28$ ns, $\eta^2 = .02$
	420–930 ms, CP3 Young: 0.92 (.88); Older: -1.28 (1.85) (1) $F(1, 18) = 15.35^{**}$, $\eta^2 = .46$ (2) $F(34, 612) = 1.7$ ns, $\eta^2 = .08$ (3) $F(34, 612) = 1.53^*$, $\eta^2 = .10$	520–950 ms, CPz Young: 0.88 (1.33); Older: -1.98 (2.5) (1) $F(1, 18) = 10.1^{**}$, $\eta^2 = .36$ (2) $F(34, 612) = 2.01^{**}$, $\eta^2 = .10$ (3) $F(34, 612) = 4.3^{***}$, $\eta^2 = .19$
	1,050–2,100 ms, CP4 Young: 1.30 (1.54); Older: -1.64 (1.71) (1) $F(1, 18) = 10.24^{**}$, $\eta^2 = .36$ (2) $F(34, 612) = 3.31^{***}$, $\eta^2 = .16$ (3) $F(34, 612) = 2.7^{***}$, $\eta^2 = .13$	1,000–2,100 ms, PO8 Young: 0.85 (1.34); Older: -2.08 (1.81) (1) $F(1, 18) = 12.01^{**}$, $\eta^2 = .40$ (2) $F(34, 612) = 4.4^{***}$, $\eta^2 = .20$ (3) $F(34, 612) = 2.21^{***}$, $\eta^2 = .11$
	2,200–2,500 ms, POz Young: 9.22 (6.46); Older: 1.37 (3.6) (1) $F(1, 18) = 7.26^*$, $\eta^2 = .29$ (2) $F(25, 450) = 8.4^{***}$, $\eta^2 = .32$ (3) $F(25, 450) = 3.23^{***}$, $\eta^2 = .15$	
LVF	180–250 ms, PO8 Young: 1.11 (1.42); Older: -1.87 (2.83) (1) $F(1, 18) = 5.85^*$, $\eta^2 = .24$ (2) $F(34, 612) = 3.5^{***}$, $\eta^2 = .16$ (3) $F(34, 612) = 0.85$ ns, $\eta^2 = .04$	220–330 ms, CP6 Young: 1.26 (1.63); Older: -1.98 (2.14) (1) $F(1, 18) = 11.53^{**}$, $\eta^2 = .39$ (2) $F(59, 1062) = 1.6$ ns, $\eta^2 = .06$ (3) $F(59, 1062) = 2.92^{***}$, $\eta^2 = .14$
	750–2,150 ms, P6 Young: 0.69 (1.27); Older: -2.87 (2.76) (1) $F(1, 18) = 8.76^{**}$, $\eta^2 = .33$ (2) $F(34, 612) = 4.2^{***}$, $\eta^2 = .19$ (3) $F(34, 612) = 1.85^{**}$, $\eta^2 = .10$	430–720 ms, Pz Young: 1.27 (1.94); Older: -1.73 (2.07) (1) $F(1, 18) = 9.58^{**}$, $\eta^2 = .35$ (2) $F(34, 612) = 1.1$ ns, $\eta^2 = .06$ (3) $F(34, 612) = 0.78$ ns, $\eta^2 = .04$
	2,220–2,540 ms, P7 Young: 6.58 (5.46); Older: 0.01 (5.00) (1) $F(1, 18) = 7.66^{**}$, $\eta^2 = .30$ (2) $F(34, 612) = 6.23^{***}$, $\eta^2 = .26$ (3) $F(34, 612) = 1.43$ ns, $\eta^2 = .07$	750–950 ms, P6 Young: 0.26 (2.27); Older: -2.38 (1.82) (1) $F(1, 18) = 6.49^*$, $\eta^2 = .26$ (2) $F(25, 450) = 1.1$ ns, $\eta^2 = .06$ (3) $F(25, 450) = 1.18$ ns, $\eta^2 = .06$

Notes. $^{***}p < .0001$, $^{**}p < .01$, $^*p < .05$.

amplitude, FC4: 7.4 ± 1.5 μV) with no interaction between them ($F(11, 99) = .48$, $p = .5$, $\eta^2 = .1$) that indicated more positive mean amplitudes to cued (estimated mean: $5.04 \pm .92$ μV) than to uncued targets (estimated mean: 4.25 ± 1.18 μV).

In the LVF, the ANOVAs performed on the young participants' data showed significant effects on the mean amplitude of N1 latency range (150–200 ms) of cueing condition ($F(1, 9) = 6.61$, $p < .05$, $\eta^2 = .42$; estimated means, cued: $-2.92 \pm .66$ μV ; uncued: $-3.63 \pm .62$ μV), and electrode ($F(25, 225) = 3.67$, $p < .0001$, $\eta^2 = .29$; maximum amplitude, P3: $4.57 \pm .96$ μV) with no interaction between them ($F(25, 225) = .74$, $p = .8$, $\eta^2 = .08$).

The ANOVAs on the mean amplitudes within the latency interval corresponding to the Nd effect (250–300 ms) showed significant effects of cueing condition ($F(1, 9) = 2.59$, $p < .05$, $\eta^2 = .22$; estimated means, cued: 5.4 ± 2 μV ; uncued: 6.7 ± 2.2 μV), electrode ($F(11, 99) = 3.23$, $p < .001$, $\eta^2 = .26$) and the interaction between these two factors ($F(11, 99) = 1.89$, $p < .05$, $\eta^2 = .17$) that indicated that while in the cued condition the maximum amplitude was at CP4 electrode (6.63 ± 2.1 μV) in the uncued condition maximum amplitudes were observed at TP8 electrode (7.22 ± 2.34 μV).

In summary, the results on cueing effects in young subjects showed that IOR induced a reduction of N1 amplitude

Table 4. Target-locked ERPs. Between-subjects analyses: Age effects. Time intervals and the corresponding electrode clusters where permutation analyses showed significant differences between age groups. Results are shown for each visual field and cueing condition

	Uncued		Cued	
	Time interval (ms)	Electrode cluster	Time interval (ms)	Electrode cluster
UVF	192–630*	F7,F5,F3,F4,F6,F8,FT7,FC5,FC3,FC1,FC2,FC4,FC6,FT8,T7,C5,C3,C1,Cz,C2,C4,C6,T8,TP7,CP5,CP3,CP1,CPz,CP2,CP4,CP6,TP8,P7,P5,P3,P1,Pz,P2,P4,P6,P8,PO7,PO3,POz,PO4,PO8,O1,Oz,O2	250–650*	FC5,FC3,FC1,FCz,FC2,FC4,FC6,FT8,T7,C5,C3,C1,Cz,C2,C4,C6,T8,TP7,CP5,CP3,CP1,CPz,CP2,CP4,CP6,TP8,P7,P5,P3,P1,Pz,P2,P4,P6,P8,PO7,PO3,POz,PO4,PO8,O1,Oz,O2
LVF	210–590*	F7,F5,F4,F6,F8,FT7,FC5,FC3,FC1,FC2,FC4,FC6,FT8,T7,C5,C3,C1,Cz,C2,C4,C6,T8,TP7,CP5,CP3,CP1,CPz,CP2,CP4,CP6,TP8,P7,P5,P3,P1,Pz,P2,P4,P6,P8,PO7,PO3,POz,PO4,PO8,O1,Oz,O2	300–650 [#]	F7,F8,FT7,FC6,FT8,T7,C5,C3,C1,C4,C6,T8,TP7,CP5,CP3,CP1,CPz,CP2,CP4,CP6,TP8,P7,P5,P3,P1,Pz,P2,P4,P6,P8,PO7,PO3,POz,PO4,PO8,O1,Oz,O2

Notes. * $p < .01$, [#] $p < .05$.

that comprised a slightly longer time interval, and a more posterior scalp distribution in the LVF than in the UVF. IOR also caused amplitude shifts during the rising part of P3 that consisted in a negative shift at posterior electrodes in the LVF, and a positive and later shift at anterior electrodes in the UVF.

Older Participants

For the older participants the results of cluster-based permutation analysis in the latency range of N1 were similar to those of the young group although the differences between cued and uncued conditions occurred within longer time intervals, and in clusters comprising more electrode sites (see Table 5, and voltage and statistic maps in Figure 4). Specifically, the ERPs in the UVF showed significant differences from 160 to 230 ms, and in the LVF the differences were significant between 150 and 250 ms. In both visual fields the differences were due to reduced N1 amplitudes to cued targets (Figure 4). Differences were also observed in the rising period of P3, but only in the UVF (Table 5 and Figure 4), where the ERPs to cued targets showed a positive shift (the Pd effect observed in the young participants) from 300 to 350 ms in a cluster comprising more electrodes than in the younger adults (see Table 5 and voltage maps in Figure 4).

Repeated measures ANOVAs with cueing condition (cued vs. uncued) and electrode (the electrodes included in the corresponding cluster) performed for each visual field separately on the mean amplitudes of each time interval and electrode showed, in the UVF, significant effects of cueing condition in the N1 latency range (160–230 ms) that indicated lower mean amplitudes to cued targets ($F(1, 9) = 10.97$, $p < .01$, $\eta^2 = .55$; estimated means, cued: $-0.74 \pm 1.04 \mu\text{V}$; uncued: $-2.05 \pm 1 \mu\text{V}$). The electrode also showed significant effects ($F(27, 243) = 9.97$, $p < .0001$, $\eta^2 = .53$) that indicated maximum amplitudes at P8 (estimated mean: $-3.4 \pm .71 \mu\text{V}$). The interaction between electrode and cueing condition was also significant ($F(27, 243) = 2.09$, $p < .01$, $\eta^2 = .19$) although maximum amplitudes were observed at P8 electrode both to cued ($-2.49 \pm 2.9 \mu\text{V}$) and to uncued targets ($-4.31 \pm 1.86 \mu\text{V}$). In this visual field, the ANOVA on the latency range corresponding to the Pd effect (300–350 ms) showed significant effects of cueing condition ($F(1, 9) = 18.27$, $p < .01$, $\eta^2 = .67$; estimated means, cued: $2.2 \pm 1.3 \mu\text{V}$; uncued: $.72 \pm 1.2 \mu\text{V}$) and electrode ($F(33, 297) = 1.57$, $p < .05$, $\eta^2 = .15$; maximum amplitude, AF3: $2.29 \pm 1 \mu\text{V}$). No interaction was found between electrode and cueing condition ($F(33, 297) = 1.45$, $p = .06$, $\eta^2 = .14$).

Finally, the ANOVA on the latency interval of N1 (150–250 ms) in the LVF showed significant effects of cueing ($F(1, 9) = 10.98$, $p < .01$, $\eta^2 = .55$) that indicated lower mean amplitudes to cued targets (estimated means, cued: $-.94 \pm 1.12 \mu\text{V}$; uncued: $-2.67 \pm .84 \mu\text{V}$). The electrode ($F(31, 279) = 9.09$, $p < .0001$, $\eta^2 = .5$) and the interaction between electrode and cueing condition ($F(31, 279) = 1.6$, $p < .05$, $\eta^2 = .15$) were also significant.

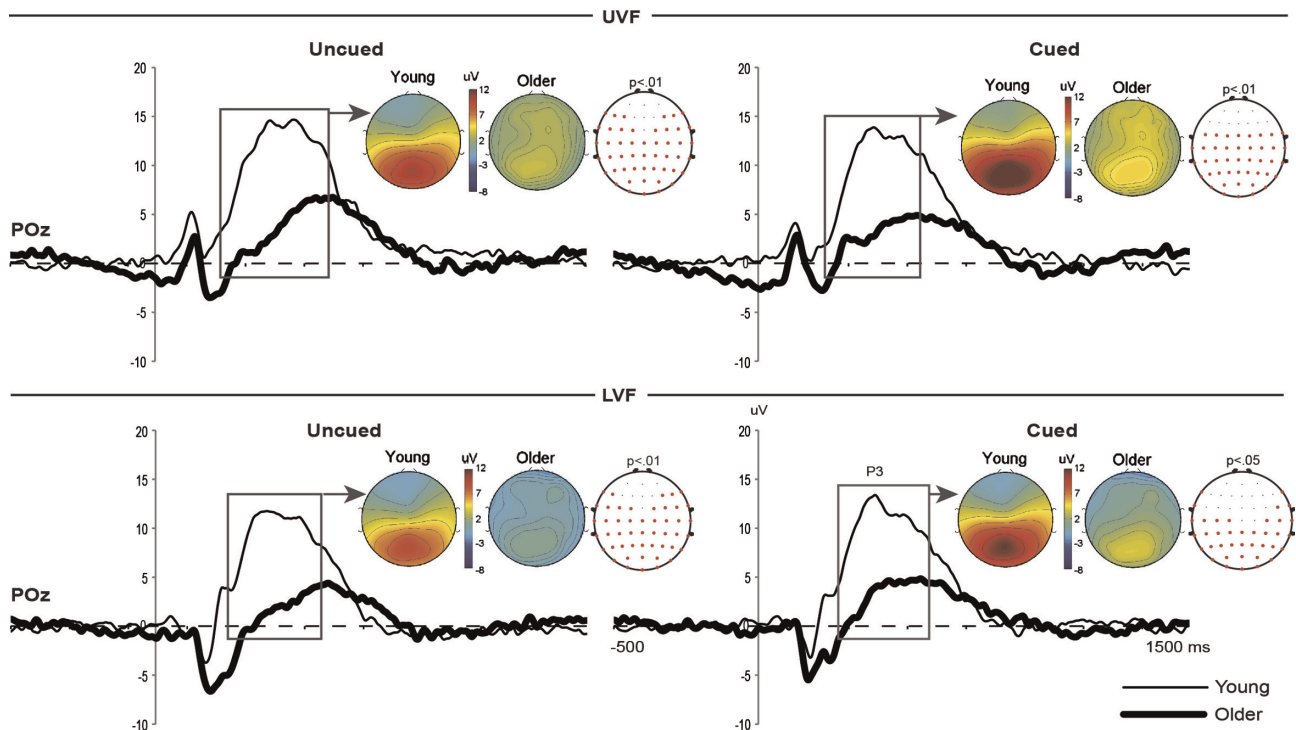


Figure 3. Target-locked ERP waveforms superimposed for each age group across visual fields and cueing conditions, and the corresponding voltage maps. Grey rectangles indicate the time intervals where significant differences were found by permutation analyses. Maps with red dots indicate the electrode sites where significant differences were observed in those time intervals.

Table 5. Target-locked ERPs. Within-subjects analyses: Cueing effects. Time intervals and the corresponding electrode clusters where permutation analyses showed significant differences between cueing conditions in each age group. Results are shown for each visual field and age group

	Cued-Uncued	
	Time interval (ms)	Electrode cluster
UVF		
Young	150–180*	AF3,AFz,F3,Fz,F2,F4,FC1,FCz,FC2,FC4,FC6
	340–360*	AF3,AFz,AF4,F3,F1,Fz,F2,F4,FC3,FC1,FC2,FC4
Older	160–230*	AF3,AFz,AF4,F3,F1,Fz,F2,F4,F6,FC3,FC1,FCz,FC2, C3,C1,Cz,C2,CP1,CPz,CP2,CP4,Pz,P2,P4,PO4,P8,PO8,O2
	300–350*	AF3,F3,F1,FC5,FC3,FC1,FCz,FC2,C3,C1,Cz,C2,CP3, CP1,CPz,CP2,CP4,P7,P5,P3,P1,Pz,P2,P4,P6,P8,PO7, PO3,POz,PO4,PO8,O1,Oz,O2
LVF		
Young	150–200*	AFz,AF4,F3,F1,Fz,F2,F4,FC1,FCz,FC2,C3,C1,Cz,C2,C4,C6,CP5, CP3,CP1,CPz,CP6,P7,P5,P3,P1,PO7
	50–300*	CP4,TP8,P7,P5,P3,P4,P6,P8,PO7,PO8,O1,O2
Older	150–250*	F7,F5,F3,F1,Fz,F2,F4,F6,F8,FT7,FC5,FC3,FC1,FCz,FC2, FC4,FC6,FT8,T7,C5,C3,C1,Cz,C2,C4,C6,T8,CP6,TP8,P6,P8,PO8

Note. * $p < .0001$.

However, maximum amplitudes were observed at P6 electrode in both cued ($-3.3 \pm 3.8 \mu\text{V}$) and uncued ($-5.63 \pm 2.74 \mu\text{V}$) conditions.

The results on cueing effects in the older group showed that IOR caused N1 amplitude reductions similar to those observed in the young group, although within longer time

intervals and at more electrode sites. The IOR effects on the rising period of P3 were only observed in the UVF in this age group, and consisted in a positive shift to cued targets (Pd effect) with a widespread scalp distribution. The Nd effect found in the young participants was absent in this age group.

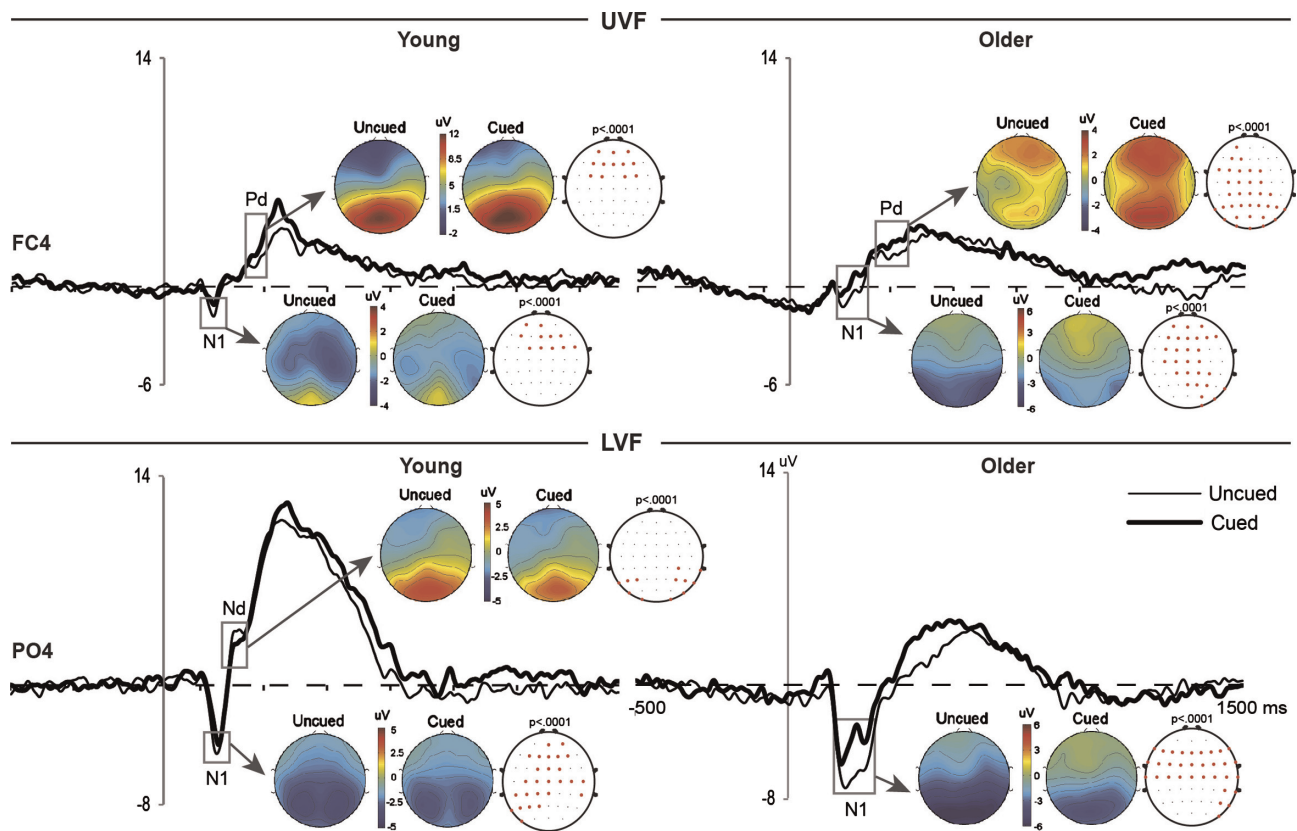


Figure 4. Target-locked ERP waveforms superimposed for each cueing condition across age groups and visual fields, and the corresponding voltage maps. Grey rectangles indicate the time intervals where significant differences were found by permutation analyses. Maps with red dots indicate the electrode sites where significant differences were observed in those time intervals.

Table 6. Response-locked ERPs (LRP). Between-subjects analyses: Age effects. Time intervals and the corresponding electrode clusters where permutation analyses showed significant differences between age groups. Results are shown for each visual field and cueing condition

	Uncued		Cued	
	Time interval (ms)	Electrode cluster	Time interval (ms)	Electrode cluster
UVF	−324 to −92*	FT7,FC5,FC3,FC1,C5,C3,C1,TP7,CP5,CP3,CP1	−200 to −100*	F7,F5,F3,FT7,FC5,FC3,FC1,C5,C3,C1,TP7,CP5,CP3,CP1
LVF	−338 to −60*	F5,FC5,FC3,C5,C3,C1,CP5,CP3,CP1	−256 to −128*	FT7,FC5,FC3,FC1,C5,C3,C1,TP7,CP5,CP3

Response-Locked ERPs

Between-Group Analyses: Age Effects

Permutation analyses on the LRP waveforms comparing age groups across visual fields and cueing conditions showed higher negative amplitudes in the older group in both visual fields and in both cueing conditions within the time intervals and the lateralized electrodes included in Table 6 (see also Figure 5). The mean amplitude values within these latency intervals and the corresponding electrodes were submitted to repeated measures ANOVAs for

each visual field separately with age group (young, older) as the between-subjects factor, and cueing condition (cued vs. uncued) and electrode (FC5-FC6, FC3-FC4, C5-C6, C3-C4, CP5-CP6, CP3-CP4) as within-subject factors. These analyses showed significant effects of age group in both visual fields (UVF: $F(1, 18) = 15.19$, $p < .001$, $\eta^2 = .46$; LVF: $F(1, 18) = 7.98$, $p < .01$, $\eta^2 = .31$) due to higher LRP amplitudes in the older group (estimated means, UVF young: $-.31 \pm .18 \mu\text{V}$, older: $-1.33 \pm .18 \mu\text{V}$; LVF young: $-.06 \pm .24 \mu\text{V}$, older: $-1.02 \pm .24 \mu\text{V}$). Cueing condition did not show significant effects on these time intervals (UVF: $F(1, 18)$, $p = .1$, $\eta^2 = .14$; LVF:

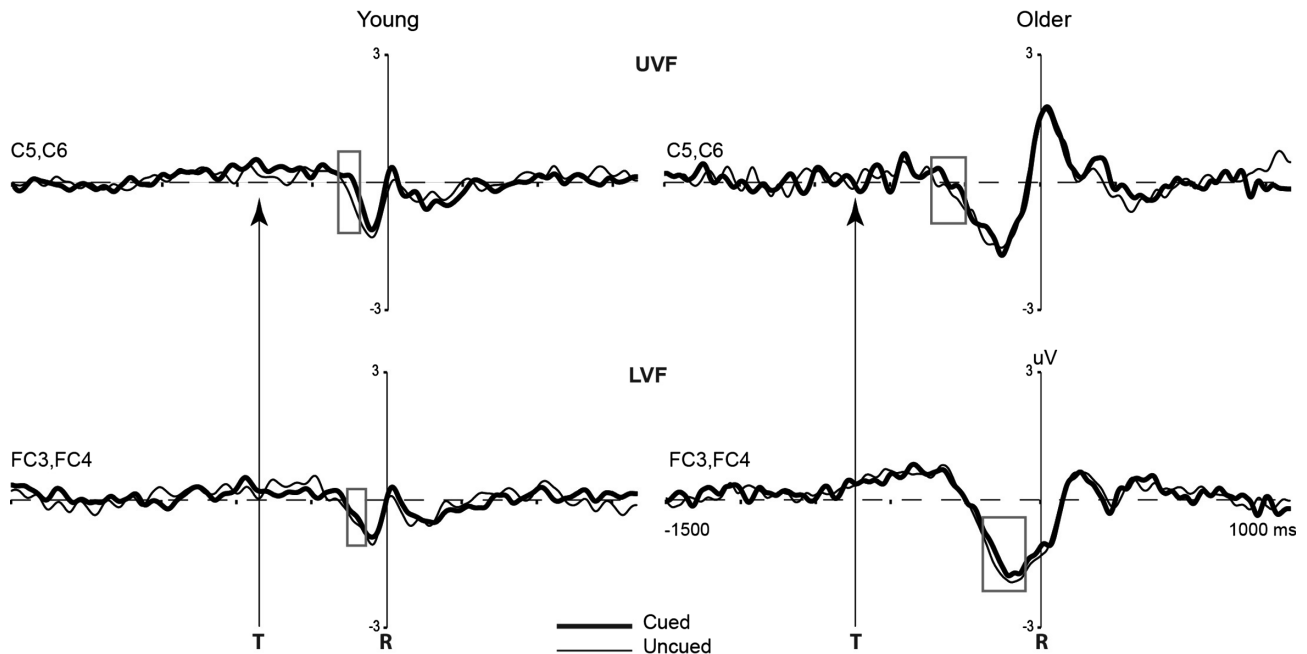


Figure 5. Response-locked ERP waveforms showing the LRP superimposed for each age group across visual fields and cueing conditions. Grey rectangles indicate the time intervals where significant differences were found by permutation analyses.

Table 7. Response-locked ERPs (LRP). Within-subject analyses: Cueing effects. Time intervals and the corresponding electrode clusters where permutation analyses showed significant differences between cueing conditions in each age group. Results are shown for each visual field and age group

	Cued-Uncued	
	Time interval (ms)	Electrode cluster
UVF		
Young	−310 to −270*	C5,TP7,CP5,CP3,P5,P3
Older	−500 to −390*	CP5,CP3,P3,P5,P7,PO7
LVF		
Young	−150 to −120*	F7,F5,FT7,FC5,FC3,FC1
Older	−280 to −30*	F5,F3,FC5,FC3

Note. * $p < .05$.

$F(1, 18) = .75$, $p = .4$, $\eta^2 = .04$). A significant interaction between cueing condition and age group was observed in the LVF ($F(1, 18) = 5.36$, $p < .05$, $\eta^2 = .23$) indicating that while in the young group the mean amplitude of the LRP was positive in the cued condition ($.15 \pm .35 \mu\text{V}$) and negative in the uncued condition ($-.40 \pm .41 \mu\text{V}$), it was negative in both cueing conditions in the older adults (cued: $-1.12 \pm .83 \mu\text{V}$; uncued: $-2.04 \pm 1.59 \mu\text{V}$). No such interaction was found in the UVF ($F(1, 18) = 2.47$, $p = .13$, $\eta^2 = .12$). In general, the above results showed higher amplitudes of the response-locked LRP across conditions and visual fields in the older group.

Within-Group Analyses: Cueing Effects

Given the existence of different spatio-temporal patterns of cueing effects in both age groups, further cluster based permutation analyses were performed for each age group and visual field separately to examine the time intervals and electrodes with possible differences in the LRP waveforms between cued and uncued conditions. These analyses showed significant differences indicating lower LRP amplitudes when responding to cued targets in both age groups and in both visual fields (see Table 7 and Figure 5). Separate repeated measures ANOVAs on mean amplitudes within these latency intervals and the corresponding electrode sites derived from the permutation analyses were conducted for each age group and visual field with cueing condition (cued vs. uncued) and electrode (those included in the corresponding cluster) as within-subject factors. The results are described in the following two sections.

Young Participants

In the young adults, significant effects of cueing were found in both visual fields (UVF, $F(1, 9) = 12.8$, $p < .01$, $\eta^2 = .59$; LVF, $F(1, 9) = 5.35$, $p < .05$, $\eta^2 = .37$) and indicated reduced LRP amplitudes to responses prepared to cued targets (UVF, estimated means, cued: $.67 \pm .69 \mu\text{V}$, uncued: $-.36 \pm .37 \mu\text{V}$; LVF, cued: $.15 \pm .35 \mu\text{V}$, uncued: $-.4 \pm .41 \mu\text{V}$). No effects of electrode (UVF, $F(5, 45) = 1.2$, $p = .32$, $\eta^2 = .12$, $\varepsilon = .42$; LVF, $F(5, 45) = .62$, $p = .7$, $\eta^2 = .06$, $\varepsilon = .49$) or the interaction

between electrode and cueing condition were found (UVF, $F(5, 45) = .86$, $p = .45$, $\eta^2 = .09$, $\varepsilon = .47$; LVF, $F(5, 45) = 1.56$, $p = .2$, $\eta^2 = .15$). In general, IOR caused a reduction of LRP mean amplitudes when responding to previously cued targets in both visual fields.

Older Participants

In the UVF, the older adults showed significant effects of cueing condition ($F(1, 9) = 4.89$, $p < .05$, $\eta^2 = .35$) along with non-significant effects of electrode ($F(5, 45) = 1.57$, $p = .2$, $\eta^2 = .15$) or the interaction “electrode by cueing condition”, $F(5, 45) = .86$, $p = .45$, $\eta^2 = .09$. Similarly to that found in the young group, the LRP amplitudes were lower to responses in the cued condition (estimated means, cued: $.27 \pm .79 \mu\text{V}$; uncued: $-.47 \pm .99 \mu\text{V}$). In the LVF non-significant effects of cueing were found ($F(1, 9) = 2.51$, $p = .15$, $\eta^2 = .22$), although both the electrode ($F(3, 27) = 7.65$, $p < .001$, $\eta^2 = .46$) and the interaction between electrode and cueing ($F(3, 27) = 4.1$, $p < .05$, $\eta^2 = .31$) were significant showing that the LRP was reduced when responding to cued targets at all electrodes included in the cluster (F5-F6, F3-F4, FC5-FC6, FC3-FC4) but at F5-F6 this amplitude difference did not reach statistical significance. As indicated by the above results, in older participants spatial IOR caused a reduction of LRP mean amplitudes similar to that observed in the young group.

Discussion

In the present study, the main objective was to analyze the effects of spatial IOR on behavioral execution and on EEG activity in healthy young and older adults. For that purpose, RTs, error rates, and stimulus-locked (cue-locked and target-locked) and response-locked ERPs were obtained in a cue-back task in which the target stimulus could appear at uninformative cued or uncued locations while participants were required to give a two-choice discrimination response to the color of the target stimulus (blue or red) and to ignore its spatial location. To control for possible interactions between IOR and spatial compatibility between target location and response hand (Ivanoff et al., 2002), the stimuli were presented along the vertical meridian. Moreover, as vertical asymmetries in visual processing have been reported in behavioral and psychophysiological studies (Amenedo, Pazo-Álvarez, & Cadaveira, 2007; Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2001; Gutiérrez-Domínguez et al., 2014; Karim & Kojima, 2010; Rezec & Dobkins, 2004; Thomas & Elias, 2011), we analyzed the data from the lower and the upper visual fields separately.

In general, when analyzing the results of the age-related effects, the older participants showed slower RTs, more negative cue-locked and response-locked ERPs, and a more homogeneous scalp distribution in target-locked ERPs.

When analyzing the results of spatial cueing effects, significant IOR in both RTs and ERPs was observed in the young and the older adults participating in the present study, although with different characteristics. In general, these results, supportive of preserved IOR in the older adults, are discussed in more detail in the following sections.

Behavioral Execution

As it has been generally observed in aging research, slower RTs were observed in the older participants in all conditions (see Ren, Wu, Chan, & Yan, 2013 for a recent review). Moreover, spatial cueing was associated with slower RTs in both age groups, indicating the existence of spatial IOR when the target was previously cued in young and older adults. This result is in agreement with previous findings (Castel et al., 2003; Faust & Balota, 1997; Hartley & Kieley, 1995; Langley et al., 2001, 2005, 2007; McCrae & Abrams, 2001; Poliakoff et al., 2007; Wascher et al., 2011). A significant interaction between age group and spatial cueing on the RTs to stimuli presented in the UVF indicated that the effects of IOR were of higher magnitude in the older than in the young participants in this visual field. The above effects were observed along with an absence of age or cueing effects on error rates, as it has also been frequently observed in the literature (Castel et al., 2003; Faust & Balota, 1997; Hartley & Kieley, 1995; Langley et al., 2001, 2005, 2007; McCrae & Abrams, 2001; Poliakoff et al., 2007).

The present behavioral results indicate that uninformative spatial cueing at 2,000 ms time intervals between cue and target onset caused IOR in older adults that, when the stimuli were presented in the UVF, was of higher magnitude than in young adults. An age-related increase in the magnitude of behavioral IOR has been previously found (Poliakoff et al., 2007), and with a similar cue-target interval (1,800 ms). The authors, based on previous literature about possible IOR neural mechanisms (Cassavaugh, Kramer, & Petersen, 2004; Mayer, Seidenberg, Dorfinger, & Rao, 2004; Wascher & Tipper, 2004), gave two possible interpretations to their finding. Specifically, they argued that it could be related to an increased strategic control over oculomotor capture thought to rely on projections from frontal eye fields (FEF) to superior colliculus (SC). Alternatively, they suggested that it could be due to a more controlled reallocation of attention onto the cued location after target presentation depending more on frontal and parietal cortical areas. However, behavioral data per se do not provide sufficient information to support such conclusions. Moreover, the relative role of subcortical (i.e., SC) and cortical (FEF, frontal-parietal attention networks) areas in IOR generation in the human brain is still a matter of debate (Klein, 2000; Mayer et al., 2004; Satel et al., 2012; Vivas, Humphreys, & Fuentes, 2003). The study of EEG activity by means of ERPs, as it will be discussed in the following sections, has helped to interpret the classical behavioral findings in the context of IOR research, although no consensus has still been reached.

ERP Results

Cue-Locked ERPs

Older participants showed significantly higher negative amplitudes in the cue-locked ERP waveforms in both visual fields and in cued and uncued trials. These higher negative amplitudes suggest more engagement of attention onto the cue in the older adults compared to the younger, whose ERPs showed in general more positive amplitude deflections in the interval between cue and target presentations (see Figure 2). The most accepted interpretation of the age-related behavioral effects of IOR suggests that they are associated with an impaired and/or delayed disengagement of attention from the cue (Castel et al., 2003; Langley, Gayzur, Saville, Morlock, & Bagne, 2011). Moreover, a recent ERP study focusing on the cue-locked frontocentral N2 found that this component was absent in the older participants (Wascher et al., 2011). The authors interpreted this result as an index of a reduced age-related inhibitory control of the processing of the cue resulting in a processing of that irrelevant stimulus as if it was relevant. The present results give support to such interpretations and they add complementary information on the possible underlying mechanisms and their implications. In this sense, Langley, Friesen, et al. (2011), when discussing whether the age differences in reflexive orienting represent an adaptive or maladaptive change for the older adults, suggested that while enhanced orienting toward valid cues can help older adults more rapidly localize important information, which could be adaptive in real-life situations, more attentive processing of invalid cues hinders attentional shifts to desired target locations. These alterations have implications for spatial orienting in the real world, particularly in situations in which misleading visual cues automatically capture older adult's attention but do not predict the location of desired information. Following Langley's argumentation, the age-related changes observed under IOR (enhanced orienting to uninformative cues) could be maladaptive to real life situations. Mayer et al. (2004) suggested that, under normal circumstances inhibitory processes are already activated after the presentation of the cue, regardless of the final location of the target, but if the target is presented at the cued (inhibited) location, an additional set of processes are initiated in order to reallocate attention to the inhibited area of space. In this context, the age-related increased and sustained negativity after cue presentation observed in the present data at central-parietal-occipital electrodes, indicative of enhanced allocation of attention and decreased or absent inhibition in the older participants, could have compensatory consequences when the target appears at cued locations because it would help in reallocating attention onto a target appearing at previously explored locations.

An alternative but non-exclusive explanation would be related to response selection and preparation after cue presentation. The higher negative amplitudes observed in the older adults and their scalp distribution (Figure 2) could be indicating that these participants processed the cue as a warning signal to prepare to adequately process the entire stimuli sequence (cue, cue-back, target) and select and

prepare the correct response to the target stimulus. In these sense, the cue-locked ERPs of this age group resembled CNV-like waveforms (Brunia & Van Boxtel, 2001; Damen & Brunia, 1994; Gómez, Marco, & Grau, 2003; Rohrbaugh & Gaillard, 1983; Walter, Cooper, Aldridge, McCallum, & Winter, 1964) that were absent in the young group, and which may suggest more effortful task-set maintenance, higher pre-activation of sensory and motor related processes, and/or more anticipatory task preparation (Kray, Eppinger, & Mecklinger, 2005; Wild-Wall, Hohnsbein, & Falkenstein, 2007).

Target-Locked ERPs

In the target-locked ERP waveforms an age-related decrease in amplitude, and a more homogeneous scalp distribution was observed across conditions and visual fields within latency ranges corresponding to the beginning part and peak resolution of the P3 component. These results agree with those well established and frequently found on P3 in aged samples (see Friedman, 2003 for a review; Friedman, Kazmerski, & Fabiani, 1997) and indicate a more effortful evaluation of target stimuli during the task (Amenedo & Díaz, 1998).

Significant effects of spatial cueing were observed on both age groups and visual fields in the N1 latency range of target-locked ERPs, showing lower amplitudes when the target was cued. During the P3 rising period, the young subjects showed different effects of spatial cueing depending on visual field. Specifically, in the UVF a positive shift (Pd effect) to cued targets was found at anterior electrodes, while in the LVF a negative shift (Nd effect) was observed at earlier time intervals and at more posterior electrodes to cued targets. However, in the older group only the Pd effect to cued targets was observed in the UVF. These results are discussed in more detail in the following paragraphs.

In the present study, the earliest effect of IOR on ERPs was in the N1 latency range in both age groups. Previous results with young adult samples, although with discrepancies, showed amplitude modulations at earlier time intervals, specifically at P1 latency. Regarding this, there are studies that have found P1 reductions under IOR conditions (Chica & Lupiáñez, 2009; McDonald et al., 1999; Prime & Jolicoeur, 2009; Prime & Ward, 2004, 2006; Tian, Klein, et al., 2011; Tian & Yao, 2008; Wascher & Tipper, 2004). Such a reduction was generally related to an inhibition of the processing of previously cued stimuli in visual areas (Wascher & Tipper, 2004), suggesting that this variation at early stages of visual processing indicates a possible causal role of P1 in IOR (Prime & Ward, 2006). However, other studies did not find P1 reductions associated with IOR (Gutiérrez-Domínguez et al., 2014; Hopfinger & Mangun, 2001; Satel et al., 2012), or even they found differences in P1 amplitude when behaviorally IOR effect was not present (Doallo et al., 2004; Eimer, 1994; Hopfinger & Mangun, 1998). The present study agrees with those that have not found IOR effects on P1 component. A recent research by Satel et al. (2012) offers an interesting explanation of these discrepancies.

Satel et al. (2012) aimed at examining whether the P1 modulations by spatial IOR are associated with retinotopic or with spatiotopic reference frames employed to inhibit the visual processing of previously cued targets. To fulfill this objective, they manipulated retinal and environmental coordinates in the visual field to dissociate spatiotopic (environmental) from retinotopic (retinal) reference frames by introducing an eye movement between the cue and the target onset. They found that early ERP reductions (P1) were more closely related to retinotopic than spatiotopic cueing effects, whereas later effects such as the Nd effect were associated with spatiotopic IOR. Taking this into account, P1 might reflect other phenomena involved in visual information filtering, inhibiting irrelevant features or increasing the signal-to-noise ratio to allow an early categorization of the stimulus in the visual system (Chica, Lasaporana, Lupiáñez, Doricchi, & Bartolomeo, 2010; Klimesch, 2011).

The results regarding IOR effects on N1 component in young adults are also divergent in the literature. Different patterns have been observed in N1 amplitude modulations associated with IOR. Thus, spatial IOR has been found to increase N1 amplitude (Tian & Yao, 2008), to decrease it (Gutiérrez-Domínguez et al., 2014; Prime & Jolicoeur, 2009; Prime & Ward, 2004, 2006; Prime et al., 2006), or even to not affect it (Hopfinger & Mangun, 2001; Van der Lubbe et al., 2005; Wascher & Tipper, 2004). In the present study, the effect of spatial IOR resulted in a reduction of its amplitude under spatial cueing conditions in both young and older participants, with differences in its scalp distribution in each visual field only in the young adults (more restricted to frontal and central-frontal electrodes in the UVF, and spreading to more posterior parietal and occipital sites in the LVF). These results agree with those of Gutiérrez-Domínguez et al. (2014), of Prime and Ward (2004, 2006) and of Prime and Jolicoeur (2009). Prime and Ward (2006) suggested three possible causes of N1 reductions: the presence of a cue-back event, the vertical arrangement of stimuli, and the use of long CTOAs. Reviewing more closely the studies on N1 modulations associated to IOR, a design characteristic shows up that may better explain these divergent effects. Specifically, a target detection task was employed in the studies that found no N1 modulations (Hopfinger & Mangun, 2001; Van der Lubbe et al., 2005; Wascher & Tipper, 2004), while a discrimination task was required in studies that found N1 reductions (Gutiérrez-Domínguez et al., 2014; Prime & Jolicoeur, 2009; Prime & Ward, 2004, 2006). Previous experiments in the context of visuospatial attention have found N1 amplitude modulations to be related to visual discrimination processes (Van der Lubbe et al., 2005; Vogel & Luck, 2000). Taking this into account, it seems likely that N1 is modulated by spatial IOR if discrimination mechanisms are acting, as in the present study, but not if only a detection process is required.

Besides P1 and N1 components, several differential waves have been analyzed as IOR indexes resulting from spatial cueing effects on ERP amplitudes falling within latency intervals that did not coincide specifically with the peak of any component (Eimer, 1994; Gutiérrez-

Domínguez et al., 2014; McDonald et al., 1999; Prime & Jolicoeur, 2009; Prime & Ward, 2004, 2006; Tian, Chica, et al., 2011; Wascher & Tipper, 2004). Among these waves, three of them share polarity (more negative under IOR effects, called in this case Nd), distribution (parietal and occipital regions), latency (approximately 200–300 ms), and association with behavioral spatial IOR effects: the Nd310 observed in Wascher and Tipper (2004), the Nd in Gutiérrez-Domínguez et al. (2014) and in Satel et al. (2012), and the Nd240 and Nd280 in Tian, Chica, et al. (2011). Moreover, in Gutiérrez-Domínguez et al. (2014), and in Tian, Chica, et al. (2011), a positive difference in amplitude (called Pd and Pd200, respectively) was also observed associated with behavioral IOR effects. In the present study both types of effects (Nd and Pd) were observed in young participants associated with spatial IOR, although they were dependent on the visual field, and only the Pd effect was observed in the older group. Specifically, in the LVF an Nd effect similar to the aforementioned differential negative waves was observed within similar latency ranges and scalp distribution. However, in the UVF the difference in amplitude between spatially cued and uncued conditions appeared slightly later, in more anterior electrode sites, and with positive polarity (Pd effect). Nevertheless, the target-locked ERPs in the older group only showed this later Pd effect, and with a more widespread scalp distribution than in the young group (see Figure 4).

Although visual spatial resolution is normally limited by factors ranging from optics to neuronal filters in the visual cortex, even in simple visual tasks (i.e., detection of lines of specific orientation), better performance has been repeatedly observed when attentional focus is directed to stimuli. This effect has been termed attentional resolution, and it is larger when the stimuli are presented in the lower visual field (Cavanagh, He, & Intriligator, 1999; He, Cavanagh, & Intriligator, 1996). It has been suggested that this lower visual field advantage in attentional resolution may be partly due to the fact that this visual field is represented in the upper part of the visual cortex, which is anatomically adjacent to and projects more heavily to the occipital-parietal regions that are often linked to spatial attentional control (Gazzaniga & Ladavas, 1987; Maunsell & Newsome, 1987; Posner, Walker, Friedrich, & Rafal, 1987). Moreover, studies on visuospatial attention have found that spatial attention guided by exogenous orienting (peripheral cues) increases the apparent contrast of visual stimulus (Carrasco, Ling, & Read, 2004; Fuller, Rodríguez, & Carrasco, 2008), and this effect has been found to be greater in the lower visual field (Fuller et al., 2008).

Taking the above into account, the Nd observed here in the LVF in young subjects could be interpreted as an N2-like effect reflecting a re-focusing of spatial attention into a target stimulus appearing in the visual field with higher attentional resolution at a location where discrimination processes had been previously inhibited (Hopf et al., 2000, 2004; McDonald et al., 2009). The positive deflection observed in the UVF under spatial IOR, with a later latency and a more anterior scalp distribution than the Nd observed in the LVF, might be related to the elicitation of an orienting response to select a target stimulus at a previously

inhibited location. In this sense, the spatial cueing of target in the UVF could trigger an anterior P2-like effect that would be related to an extra evaluation of, and/or a conflict resolution in working memory, in trials with targets presented in previously inhibited locations (Du, Zhang, Xiao, & Wu, 2007; Gajewski, Stoerig, & Falkenstein, 2008; Potts, 2004). In this context, the age-related absence of the Nd effect observed in the LVF (in fact, although non-significant, a Pd-like effect was also observed in this visual field in the older group, see Figure 4) along with the presence of the Pd effect in the UVF could be related to a poorer attentional resolution in the LVF, and to a more effortful extra evaluation of targets presented in previously cued locations in the UVF in the older group.

Response-Locked ERPs

The response-locked ERP (LRP) waveforms were more negative in the older group across visual fields and cueing conditions, a finding that is in agreement with the previous research on the age-related changes in the LRP component (Falkenstein et al., 2006; Roggeveen, Prime, & Ward, 2007; Vallesi & Stuss, 2010; Yordanova, Kolev, Hohnsbein, & Falkenstein, 2004), and that has been interpreted as a functional dysregulation during response programming in the older brains (Yordanova et al., 2004).

Besides this age-related increase in the LRP amplitude, both young and older participants showed lower LRP amplitudes when preparing correct responses to cued targets (see Figure 5). Previous research on LRP changes under spatial IOR has concluded that spatial IOR does not affect motor processes (Prime & Ward, 2004, 2006). However, recent reports analyzing time-frequency changes in EEG activity under spatial IOR found significant changes in movement-related frequency bands that were interpreted as less motor preparation due to either sensorimotor idling (Amenedo et al., 2013) and/or motor inhibition (Amenedo et al., 2013; Pastötter et al., 2008) when responding to previously cued targets. The present IOR-related reduction in LRP amplitudes is in agreement with the above suggestions, and indicates that spatial IOR affects not only stimulus processing but also response preparation by inhibiting or reducing it to targets appearing at previously cued locations. Moreover, these spatial IOR effects on response preparation were observed independently of the age effects, which in general agrees with previous results showing IOR effects on movement-related frequency EEG bands in older adults (Amenedo et al., 2013).

Conclusion

In summary, the results of this study, which agree with the general finding of preserved behavioral IOR effects, add information on their possible neural correlates. Specifically, the results of the analyses of cueing effects on stimulus-locked and response-locked ERPs showed that the older adults inhibit or reduce the processing of targets appearing

at cued locations, and the preparation to respond to them but with the added cost of allocating more attentional resources onto the cue (possibly to use it as a warning signal), and maintaining a more effortful processing during all the stimulus sequence within the trial.

Ethics and Disclosure Statements

Informed consent was obtained from all participants.

All authors disclose no actual or potential conflicts of interest including any financial, personal, or other relationships with other people or organizations that could inappropriately influence (bias) their work.

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