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Age-related differences in bottom-up and top-down attention: Insights from EEG and MEG

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Abstract

Attention operates through top-down and bottom-up processes, and a balance between these processes is crucial for daily tasks. Imperilling such balance could explain ageing-associated attentional problems such as exacerbated distractibility. In this study, we aimed to characterize this enhanced distractibility by investigating the impact of ageing upon event-related components associated with top-down and bottom-up attentional processes. MEG and EEG data were acquired from 14 older and 14 younger healthy adults while performing a task that conjointly evaluates top-down and bottom-up attention. Event-related components were analysed on sensor and source levels. In comparison with the younger group, the older mainly displayed (1) reduced target anticipation processes (reduced CMV), (2) increased early target processing (larger P50 but smaller N1) and (3) increased processing of early distracting sounds (larger N1 but reduced P3a), followed by a (4) prolonged reorientation towards the main task (larger RON). Taken together, our results suggest that the enhanced distractibility in ageing could stem from top-down deficits, in particular from reduced inhibitory and reorientation processes.

KEYWORDS
ageing, distractibility, ERF, ERP, MEEG, P3a, RON, source localization

1 | INTRODUCTION

Our environment contains far more information than we can process at any one time. Thus, we depend on attention to orient our limited resources towards relevant items (Desimone & Duncan, 1995; Reynolds & Heeger, 2009). Attention can be oriented either in a top-down (endogenous) manner, for example, in anticipation of relevant stimuli, or in a bottom-up (exogenous) manner, for example, attentional capture by task-irrelevant salient stimuli. A good balance between these mechanisms is crucial to be task-efficient while remaining

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Abbreviations: CAT, competitive attention task; CMV, contingent magnetic variation; CNV, contingent negative variation; cueRRs, cue-related responses; dis1RRs, early distracting sound-related responses; ERFs, event-related fields; ERPs, event-related potentials; FEF, frontal eye fields; IPS, intraparietal sulcus; lPFC, lateral prefrontal cortex; MMSE, Mini-Mental State Examination; RON, reorienting negativity; rTPJ, right temporoparietal junction; targetRRs, target-related responses; VFC, ventral frontal cortex.

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aware, yet not fully distracted, of our surroundings. The tendency to have one's attention captured in such fashion is referred to as distractibility. Increased distractibility can result from either a reduced efficiency of top-down mechanisms or an exacerbated triggering of bottom-up attentional capture (or both).

Anatomically, top-down and bottom-up orienting mechanisms are, respectively, supported by partially segregated brain networks: (1) *the dorsal frontoparietal network*, including the frontal eye fields (FEF) and the intraparietal sulcus (IPS), and (2) *the ventral frontoparietal network*, including the right temporoparietal junction (rTPJ) and the ventral frontal cortex (VFC; inferior and middle frontal gyri). These networks overlap mainly in the lateral prefrontal cortex (lPFC) (Corbetta et al., 2008; Corbetta & Shulman, 2002; Fox et al., 2006). Functionally, the deployment of top-down mechanisms, in anticipation of a target, manifests through evoked activity such as the contingent negative variation (CNV) (Bidet-Caulet et al., 2015; Brunia, 1999; Brunia & van Boxtel, 2001a; Gómez et al., 2004; Walter et al., 1964) as well as target-related activities such as the early N1/P2 (e.g. Bidet-Caulet et al., 2007; Eason et al., 1969; Hillyard, 1973; Picton & Hillyard, 1974; Slagter et al., 2016) and target P3, also denoted P3b (Bidet-Caulet et al., 2015; Desmedt et al., 1965; Golob et al., 2002; Sutton et al., 1965) components. Different stages of bottom-up mechanisms, or attentional capture, have been indexed by different distractor-related components: In particular, the P3 complex, also called P3a or novelty-P3, is deemed to index novelty detection, involuntary orienting of attention and phasic arousal (review in Escera et al., 2000; Masson & Bidet-Caulet, 2019), whereas the subsequent reorienting negativity (RON) is suggested to reflect the reorienting of attention to task-relevant information (Escera et al., 2003; Escera & Corral, 2007; Horváth, Maess, et al., 2008; Horváth, Winkler, & Bendixen, 2008).

Ageing is characterized by a decline in many cognitive processes such as working memory, executive function, language and attention and by an increased distractibility (Drag & Bieliauskas, 2010). Ageing impacts differently top-down and bottom-up mechanisms of attention (see Kok, 2000 for a review). Regarding top-down attention, there has been conflicting evidence of a reduced (e.g. Gajewski et al., 2010; Getzmann et al., 2016), a preserved (Hämmerer et al., 2010; Schmitt et al., 2014) or an amplified (Hong et al., 2015) cue-related CNV, concomitant with a reduction in the target-related P3 (e.g. Chao & Knight, 1997; Gaeta et al., 2003; Karayanidis et al., 1995; Lorenzo-López et al., 2007; Woods, 1992). Concerning bottom-up attention, a reduced P3 complex to irrelevant unexpected stimuli

(i.e. novel sounds) has been quite consistently found (Friedman & Simpson, 1994; Knight, 1987; Morrison et al., 2019; Tusch et al., 2017; but see Berti, 2013; Berti et al., 2017). However, it is debated whether this reduced response is related to (1) a deficit in involuntary shifting attention or to (2) impaired inhibitory mechanisms of top-down attentional control (Kok, 2000). Importantly, there is consistent evidence that ageing is characterized by a reduced capability to inhibit irrelevant input (Chao & Knight, 1997; Gazzaley et al., 2005; Getzmann et al., 2013; Horváth et al., 2009a; Mager et al., 2005). These deficits have been accounted for by two major hypotheses: the inhibitory deficit hypothesis (Hasher & Zacks, 1988) and the frontal hypothesis of ageing (West, 1996).

Given the aforementioned inconsistencies in the literature and scarcity of research regarding bottom-up attention, we aimed to characterize the brain origins of the exacerbated distractibility with ageing by investigating the impact of ageing on evoked (time-locked) activities supporting the balance between top-down and bottom-up attention. For this purpose, we recorded simultaneous MEG and EEG activities from younger and older participants while they were performing the competitive attention task (CAT) (Bidet-Caulet et al., 2015), a paradigm that allows the simultaneous assessment of bottom-up and top-down mechanisms of auditory attention and of the interaction between them (Figure 2). Visual cues trigger the deployment of voluntary attention in anticipation of auditory targets. In 25% of the trials, a task-irrelevant distracting sound is played between the cue and the target. The fluctuation across trials of the distractor timing onset allows to dissociate the effects of distraction and phasic arousal triggered by a distracting sound (Figure 1; Bidet-Caulet et al., 2015; ElShafei et al., 2019, 2020; Masson & Bidet-Caulet, 2019). We hypothesized that ageing would be characterized by (1) altered top-down anticipatory mechanisms, as indexed by the CNV and target-related P3, and (2) impaired bottom-up mechanisms, as indexed by the P3a and the RON evoked by distracting sounds.

2 | MATERIAL AND METHODS

2.1 | Participants

Participants were 14 younger (median age = 25.5; min = 20; max = 29; 5 female) and 14 older (median age = 66.5; min = 61; max = 75; 5 female) adults. Age inclusion criteria were age between 18 and 30 for the younger group and above 60 for the older one. The two groups were matched for sex, handedness, school and

FIGURE 1 Experimental paradigm. Top panel: Examples of informative and uninformative trials with no distracting sound (75% of all trials): a visual cue (200 ms duration) indicated, or not, in which ear (left or right) the target sound would be played (100 ms duration) after a fixed 1000-ms delay. Bottom panel: Examples of informative and uninformative trials with a binaural distracting sound (300 ms duration, 25% of all trials) between the cue and the target. The distracting sound could equiprobably occur in two different time periods after the cue offset: in the 50–350 ms range (DIS1) or in the 350–650 ms range (DIS2)
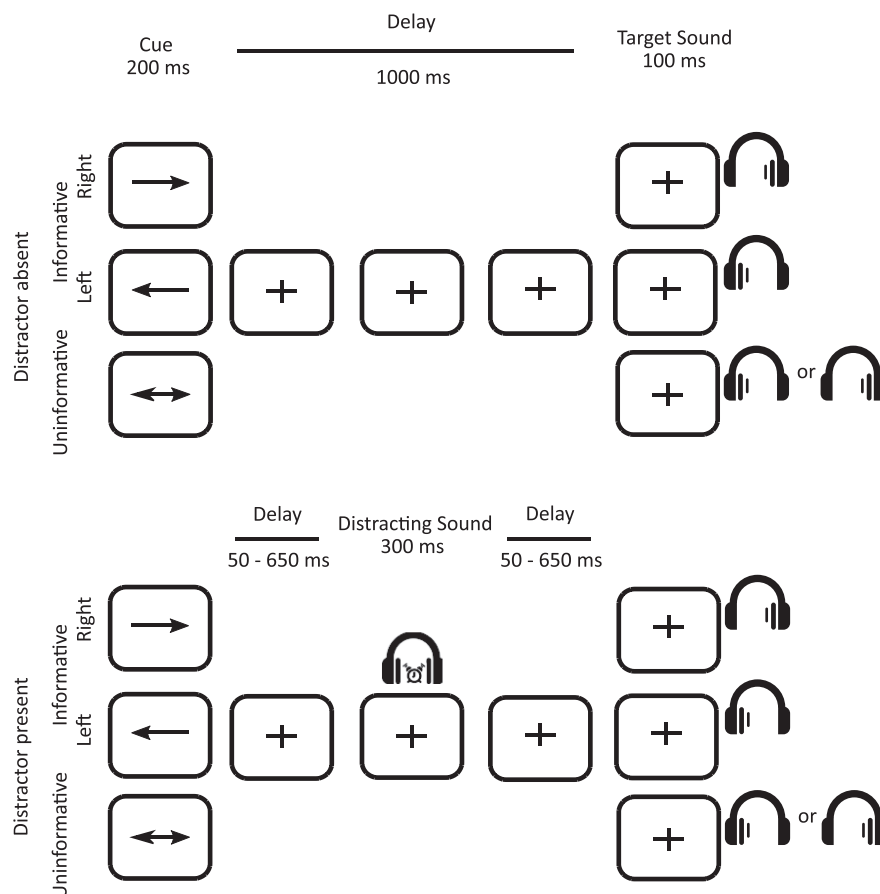
musical education. All participants were healthy, right-handed, free from any neurological or psychiatric disorders and reported normal hearing and normal or corrected-to-normal vision (see ElShafei et al., 2020 for more details). In addition, all participants performed the Mini-Mental State Examination (MMSE) (Folstein et al., 1975) in order to exclude confounds from other cognitive deteriorations, for example, dementia; and no significant difference between groups was found. Population characteristics are plotted in Figure 2. The study was approved by the local ethical committee. Participants gave written informed consent, according to the Declaration of Helsinki, and they were paid for their participation. Please note that this dataset has been included in the analysis presented in a previous study of the impact of ageing upon oscillatory activities (ElShafei et al., 2019). Data from younger participants have also been used in other studies (ElShafei et al., 2019; Masson et al., 2020).

2.2 | Stimuli and tasks

2.2.1 | CAT

Participants were instructed to categorize target sounds as either a high- or low-pitched sound. In 75% of the

trials, a target sound followed a central visual cue (200 ms duration) with a fixed delay of 1000 ms (see Figure 2). The cue was a green arrow, centrally presented on a grey-background screen, pointing either to the left, right or both sides. Target sounds were monaural pure tones (carrier frequency of 512 or 575 Hz; 100 ms duration; 5 ms rise time, 5 ms fall time). In the other 25% of trials, the same structure was retained; however, a binaural distracting sound (300 ms duration) was played during the cue–target delay (50–650 ms range after cue offset). Trials with a distracting sound played from 50 to 350 ms after the cue offset were categorized as 'DIS1', those with a distracting sound played from 350 to 650 ms after the cue offset were categorized as 'DIS2', and those with no distracting sound were categorized as 'NoDIS'. Please note that distracting sounds were uniformly paced in time between 50 and 650 ms after the cue offset. For each participant, a total of 40 different ringing sounds were used as distracting sounds (clock alarm, doorbell, phone ring, etc.) (see ElShafei et al., 2020 for more details).

The cue and target categories were manipulated in the same proportion for trials with and without a distracting sound. In 25% of the trials, the cue was pointing left, and the target sound was played in the left ear, and in 25% of the trials, the cue was pointing right, and the
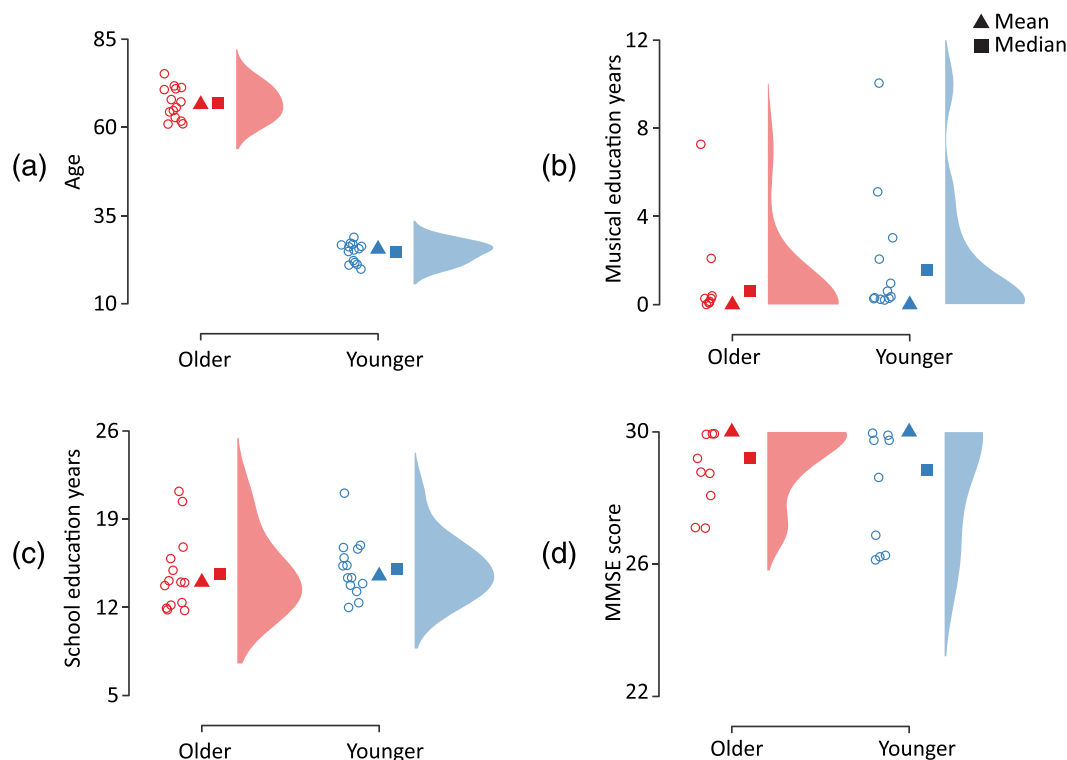
FIGURE 2 Distribution of demographic characteristics in the younger and older groups. (a) Age in years. (b) Musical education in years. (c) School education in years. (d) MMSE score. Each panel depicts a scatter plot of individual values (red for younger and blue for older) combined with median, mean values and probability density plots per group

target sound was played in the right ear, leading to a total of 50% of *informative* trials. In the other 50% of the trials, the cue was *uninformative*, that is, pointing in both directions, and the target sound was played in the left (25%) or right (25%) ear. To compare brain responses to acoustically matched sounds, the same distracting sounds were played in each combination of cue categories (*informative*, *uninformative*) and distractor condition (DIS1 or DIS2). Each distracting sound was thus played four times during the whole experiment, but no more than once during a single block, to limit habituation.

Participants were instructed to categorize two target sounds as either high- or low-pitched sound, by either pulling or pushing a joystick. The target type (high or low) was manipulated in the same proportion in all conditions. The mapping between the targets (low or high) and the responses (pull or push) was counterbalanced across participants, but did not change across the blocks, for each participant. In order to account for the participants' pitch-discrimination abilities, the pitch difference between the two target sounds was defined according to a discrimination task score (see below). Participants were informed that informative cues were 100% predictive of the ear of presentation and that a distracting sound could be sometimes

played. They were asked to allocate their attention to the cued side in the case of informative cue to ignore the distractors and to respond as quickly and correctly as possible. Participants had a fixed 3.4-s response window. In the absence of the visual cue, a blue fixation cross was presented at the centre of the screen. Participants were instructed to keep their eyes fixated on the cross.

2.2.2 | Procedure

Participants were seated in a sound-attenuated, magnetically shielded recording room, at a 50-cm distance from the screen. The response device was an index-operated joystick that participants moved either towards them (when instructed to pull) or away from them (when instructed to push). All stimuli were delivered using Presentation software (Neurobehavioral Systems, Albany, CA, USA). All sounds were presented through air-conducting tubes using Etymotic ER-3A foam earplugs (Etymotic Research Inc., USA).

First, the auditory detection threshold was determined for the two target sounds differing by two semitones (512 and 575 Hz), for each ear, for each participant using the Bekesy tracking method (Von Békésy & Wever, 1960).

Second, participants performed a discrimination task during which they were randomly presented with the target sounds equiprobably in each ear (four trials per pitch) and were asked to categorize the target sounds as either high- or low-pitched sound within 3 s. If participants failed to respond correctly to more than 85% of the trials, the pitch of the high target sound was augmented by half a semitone with a maximum difference of three semitones between the two targets (auditory detection thresholds were then measured again with the new targets).

Afterwards, participants were trained with a short sequence of the CAT. Finally, MEG and EEG were recorded while participants were performing 10 blocks (64 trials each), leading to 240 trials in the NoDIS and 80 in the DIS conditions, for informative and uninformative cues, separately. The whole session lasted around 80 min. After the MEG/EEG session, participants' subjective reports regarding their strategies were collected.

2.3 | Power analysis

We acknowledge that our sample size is relatively low. This reflects the challenges of running an auditory MEG experiment in older participants as several inclusion criteria have to be fulfilled: cognitive health, no medication affecting brain activity, no major audition problems and compatibility with MEG and MRI recordings (no metal in body). Thus, in order to give an indication of the robustness of the present statistical results, we have applied sensitivity power analysis using the G*Power software (Faul et al., 2009, 2007). According to this analysis, for unpaired two-tailed t-tests with $n = 14$ per group, power value higher than 0.8 would correspond to effect sizes (Cohen's d) superior to 1.1 and t-values superior to 2.06.

2.4 | Behavioural data analysis

For behavioural analyses, we excluded incorrect trials and compared group performances using unpaired t-tests. We tested the group effect on global performance measures (median reaction times [RTs] and percentage of correct responses) and on three specific measures of the CAT (see Figure 3) (Bidet-Caulet et al., 2015; ElShafei et al., 2020; Hoyer et al., 2021; Masson et al., 2020; Masson & Bidet-Caulet, 2019):

i. CUE BENEFIT: Estimated as the difference in median RTs between the uninformative and informative NoDIS conditions. This measure reflects the deployment of top-down processes based on the cue information to faster discriminate the target.
ii. AROUSAL BENEFIT: Estimated as the difference in median RTs between the NoDIS and DIS1 conditions.

Because distracting sounds trigger both a long-lasting increase in arousal resulting in an RT decrease and a strong short-lived attentional capture (orienting) effect associated with an RT increase (Bidet-Caulet et al., 2015; ElShafei et al., 2020; Masson & Bidet-Caulet, 2019), this measure provides a good approximation of the arousal effect.

iii. DISTRACTION COST: Estimated as the difference in median RTs between the DIS2 and DIS1 conditions. This measure provides a good approximation of the distraction effect with little contamination by arousal increases (Bidet-Caulet et al., 2015; ElShafei et al., 2020; Masson & Bidet-Caulet, 2019).

In order to correct for multiple testing (as several measures are inspected), a subsequent Bonferroni correction has been applied.

2.5 | Brain recordings

Simultaneous EEG and MEG data were recorded. MEG data were acquired with a 275-sensor axial gradiometer system (CTF Systems Inc., Port Coquitlam, Canada) with continuous sampling at a rate of 600 Hz, a 0.016- to 150-Hz filter bandwidth and first-order spatial gradient noise cancellation. The EEG data were acquired continuously at the same sampling rate from seven scalp electrodes placed at frontal (Fz, Fc1, Fc2), central (Cz) and parietal (Pz) sites, and at the two mastoids (M1, M2). Electrode placement was chosen in order to capture the well-established event-related markers of attention such as CNV, target P3 and P3 complex. The reference electrode was placed on the tip of the nose, the ground electrode on the shoulder. Moreover, eye-related movements were measured using diagonal EOG electrodes (bipolar montage). Head position relative to the gradiometer array was acquired continuously using coils positioned at three fiducial points; nasion and left and right pre-auricular points. Head position was adjusted at the beginning of each block to control head movements.

In addition to MEG and EEG recordings, T1-weighted three-dimensional anatomical images were acquired for each participant using a 3T Siemens Magnetom whole-body scanner (Erlangen, Germany). The processing of these images was carried out using CTF's software (CTF Systems Inc., Port Coquitlam, Canada). In the sensor space, MEG and EEG data preprocessing were performed using ELAN (Aguera et al., 2011), data analysis and visualization were performed using FieldTrip (Oostenveld et al., 2011), while statistical comparisons were carried out using R (R Core Team, 2014). In the source space, event-related field (ERF) reconstruction was performed using the MATLAB Brainstorm toolbox (see below).
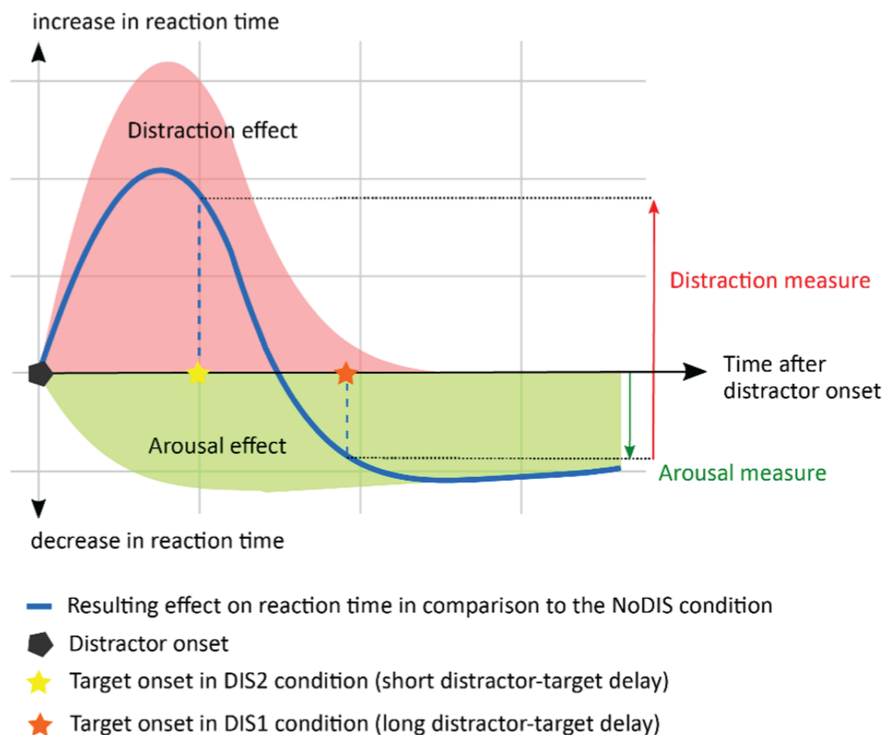
2.6 | Data pre-processing

Continuous MEG and EEG data were band-stop filtered between 47 and 53, 97 and 103 and 147 and 153 Hz (zero-phase shift Butterworth filter, order 3). For MEG data, independent component analysis was computed on bandpass filtered (0.1–40 Hz, zero-phase shift Butterworth filter, order 3) data. Subsequently, components (four on average) were removed from the band-stop filtered data via the inverse ICA transformation in order to remove eye-related (blinks and saccades) and heart-related artefacts. Eye artefacts were removed from the EEG signal by applying a linear regression based on the EOG signal.

Only correct trials were considered for electrophysiological analyses. Data segments for which the head position differed for more than 10 mm from the median position during the 10 blocks were excluded. In addition, data segments contaminated with sensor jumps, MEG or EEG muscular activity were excluded semi-automatically using a threshold of 10,000 fT, 2500 fT or 150 µV, respectively. For all participants, more than 75% of the trials remained, after rejection, for further analyses. Finally, both MEG and EEG data were bandpass filtered between 0.2–40 Hz (zero-phase shift Butterworth filter, order 3).

2.7 | Data analysis

2.7.1 | Sensor-level analysis

Event-related potentials (ERPs) and ERFs were obtained by averaging filtered MEG and EEG data locked to three events: cue-related responses (cueRRs), target (targetRRs) and early distracting sounds (dis1RRs). For cueRRs and targetRRs, a baseline correction was applied based on the mean amplitude of the −100–0 ms period before the cue and target onset, respectively. For disRRs, surrogate distractor ERFs/ERPs were created in the NoDIS trials and subtracted from the actual distractor ERFs/ERPs. The obtained distractor ERFs/ERPs were thus free of cue-related activity.

2.7.2 | Sensor-level statistics

In order to investigate the impact of ageing upon cue, target and early distracting sound-related fields, each sample in each sensor within a time window of interest (0–1200 ms post-cue, 0–600 ms post-target onset and 0–650 ms post-dis1 onset, respectively) was submitted to non-parametric permutation analysis (Maris & Oostenveld, 2007) using unpaired t-tests comparing groups. Effects were considered significant if (1) p-values remained lower than 0.05 for a minimum of 10 neighbour sensors and of nine successive time points (15 ms) (Guthrie & Buchwald, 1991) and (2) averaged effect sizes (Cohen's d) within that sensor time window were superior to 1.1 and t-values were superior to 2.06 (see section 2.3). We used a similar approach for ERPs (data in the Supporting Information).

2.7.3 | Source-level analysis

Segmentation of the individual T1-weighted MRIs was conducted using the FreeSurfer software package

(Fischl, 2012; http://surfer.nmr.mgh.harvard.edu). Segmentation was visually inspected and then imported (15,002 vertices) in the Brainstorm toolbox (Tadel et al., 2011; http://neuroimage.usc.edu/brainstorm) with which further source analyses were conducted. The white matter–grey matter boundary segmented by FreeSurfer was used as a source space for subsequent weighted minimum norm estimation. A noise covariance matrix was computed on the resting state session of the experiment, which had been preprocessed with the same pipeline than data from the task session. The forward model was computed with the OpenMEEG software (Gramfort et al., 2010; https://openmeeg.github.io/).

ERFs and MEG sensors positions were imported in Brainstorm. After co-registration between the individual anatomy and MEG sensors, cortical currents were estimated using a distributed model consisting of 15,002 currents dipoles from the time series of the 275 gradiometer signals using a linear inverse estimator (weighted minimum norm current estimate, signal-to-noise ratio of 3, whitening PCA, depth weighting of 0.5). Source orientations were constrained to the orthogonality to the grey–white matter boundary of the individual MRIs. Source maps were standardized through a z-score baseline normalization and then rectified by retaining only absolute values. Source maps were then projected on a standard brain (ICBM152) and spatially smoothed (FWHM = 3 mm) prior to group averaging and statistics.

2.7.4 | Source-level statistics

All statistical analyses at the source level were conducted using built-in statistical tools in the SPM12 toolbox (https://www.fil.ion.ucl.ac.uk/spm/software/spm12/). Source maps were exported from Brainstorm to SPM12. To investigate group differences, one-sided independent t-tests were computed on the value of source activity for each and every cortical vertex. These tests were performed in the time windows showing significant group difference at the sensor level. The direction of the unilateral tests was chosen according to the direction of the corresponding effect at the sensor level. Significance threshold was 0.05.

3 | RESULTS

3.1 | Behavioural results (Table 1, Figure 4, Figures S1 and S2)

Participants correctly performed the discrimination task in 95.37 ± 0.29 SEM % of the trials. The remaining trials were either incorrect trials (4.62 ± 0.29 SEM %), missed trials (0.49 ± 0.09%) or trials with FAs (0.14 ± 0.03%). No significant difference between groups was found in median RTs and percentage of correct responses (see Figure S1). A comprehensive analysis of median RTs can be found in the Supporting Information and in ElShafei et al. (2020).

Planned behavioural comparisons in RTs between groups demonstrated that the distraction cost (DIS2 − DIS1) was significantly more pronounced for the older group ($p_{BONFcor} = 0.012$), whereas the arousal benefit (NoDIS − DIS1) and the cue benefit (uninformative NoDIS − informative NoDIS) were not significantly different between groups ($p_{uncor} > 0.6$). In summary, the only behavioural difference between groups was a larger distraction cost displayed by the older group, that is, the older group were slower (possibly more distracted) during trials with later occurring distracting sounds. Individual values are plotted in Figures 4 and S2.

3.2 | Cue-related responses (Figure 5, Figures S3–S5)

For the MEG, in response to visual cues, the permutation analysis revealed a significant difference between groups within the time window of the CMV (600–1200 ms) at left temporal and central sensors. Corresponding individual data and effect sizes (Cohen's d) are presented in Figure S3. Source-level analysis revealed that the younger group displayed a stronger activation in the left and right postcentral gyrus and left Heschl gyrus (Brodmann area [BA] 1, 2, 3 and 41). For the EEG, no difference was found between groups at the sensor level (Figure S4).

3.3 | Target-related responses (Figure 6, Figures S6–S8)

For the MEG, in response to auditory targets, the permutation analysis revealed significant differences between groups within the time window of the P50m (20–50 ms) and the N1m (120–190 ms) at left and right occipital, central and parietal sensors. Corresponding individual data and effect sizes (Cohen's d) are presented in Figure S6. Analyses at the source level revealed that the older group displayed a stronger activation in left and right temporal and parietal cortices (BA 40, 41, 42, 43 and 44) within the P50m time window, whereas within the N1m time window, the younger group displayed a stronger activation in the left parietal cortex (BA 7).

For the EEG (Figure S7), ERPs were found larger in older than in younger within the time window of the P50

TABLE 1 Summary of the behavioural results

RT measure	Younger (mean ± SEM)	Older (mean ± SEM)	*t*-value	p_{uncor}	$p_{BONFcor}$	Cohen's *d*
Median RT (ms)	488.75 ± 25.17	553.75 ± 24.36	1.25	0.21	NA	0.37
% correct responses	97.39 ± 0.95	97.91 ± 0.92	0.59	0.55	NA	0.14
Cue benefit (ms)	7.26 ± 5.48	9.7 ± 5.8	0.3	0.76	NA	0.12
Arousal benefit (ms)	18.86 ± 7.45	23.03 ± 5.36	0.45	0.65	NA	0.17
Distraction cost (ms)	44.1 ± 6.86	84.52 ± 10.62	3.19	0.004	0.012	1.2

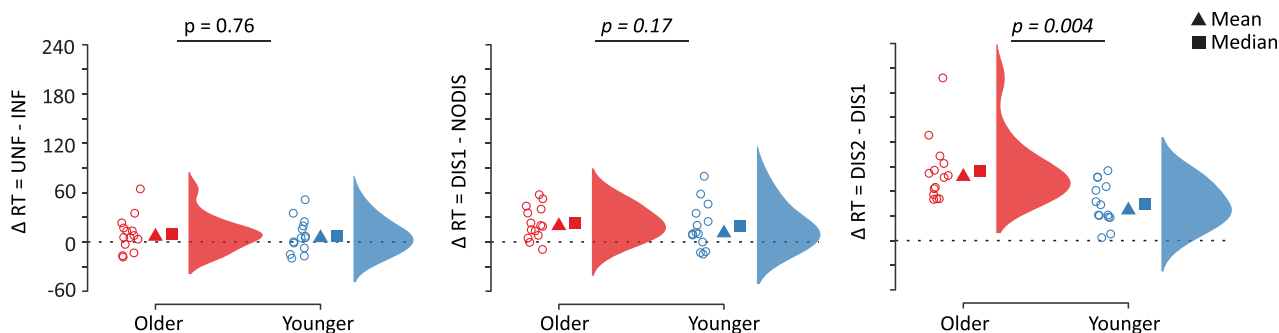*Note*: $P_{BONFcor} < 0.05$.

FIGURE 4 Group differences in behaviour. Raincloud plots depicting group differences in RT measures of the competitive attention test: (a) cue benefit, (b) arousal benefit and (c) distraction cost. *P*-values result from unpaired *t*-tests between groups. Each panel depicts a scatter plot of individual values (red for younger and blue for older) combined with median, mean values and probability density plots per group

(10–50 ms) and smaller during the time window of the target P3 (130–580ms).

3.4 | DIS1-related responses (Figure 7, Figures S9–S11)

For the MEG, in response to early distracting sounds, the permutation analysis revealed a significant difference between groups within the time window of the N1m (70–110 ms), the P3am (180–250 ms) and the RONm (450–580 ms). Corresponding individual data and effect sizes (Cohen's *d*) are presented in Figure S9. Analyses at the source level revealed that the older group displayed a stronger activation of the left and right temporal cortices (BA 40, 41 and 42) within the N1m time window and stronger activation of the right parietal cortex (BA 4 and 5) and left motor areas within the RONm time window, whereas within the P3am time window, the younger group displayed a distributed stronger activation. For the EEG (Figure S10), ERPs were found smaller in older than in younger within the time window of the P3 complex (including the P2, P3a and P3b) and larger during the time-window of the RON (420–650 ms).

4 | DISCUSSION

In the present study, we observe that ageing impacts top-down and bottom-up attentional processes differently. On the one hand, top-down target anticipation processes (CMV) were found reduced with ageing, whereas target processing was enhanced at early latencies and reduced at later ones. This was accompanied by no significant ageing difference in top-down attention at the behavioural level. On the other hand, in response to distracting sounds, an enhanced N1 (reflecting enhanced processing of task-irrelevant information), a reduced P3a (reflecting reduced deployment of inhibitory mechanisms) and an enhanced RON (reflecting prolonged reorientation towards the task) are concomitant to a larger distraction cost in RTs, in the older group.

4.1 | Impact of ageing on top-down attentional mechanisms

Contrary to previous studies (Ebaid et al., 2017; Eckert et al., 2010; Kerchner et al., 2012), no age-related decline in general behaviour (median RT and accuracy) was observed (Figure S1). In addition, in line with
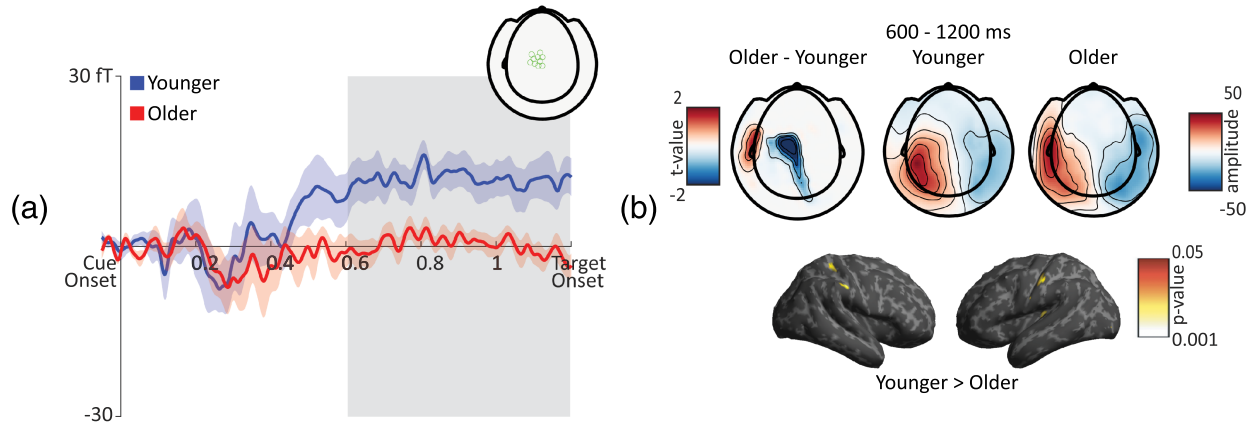
FIGURE 5 Group differences in cue-related ERFs. (a) Grand average cue-related ERFs (averaged over sensors highlighted in green) for the older (red) and younger group (blue). Shaded areas denote between-participants standard error. Grey bars indicate significant differences between groups. [b] Top row: Topographies showing statistical distribution of these significant differences in addition to grand average topographies of ERFs in each group within the time window highlighted in (a). Bottom row: *P*-value map (masked for *p* < 0.05, the whiter the lower) of the pattern of increased brain activation (source-reconstructed MEG data) in the younger group
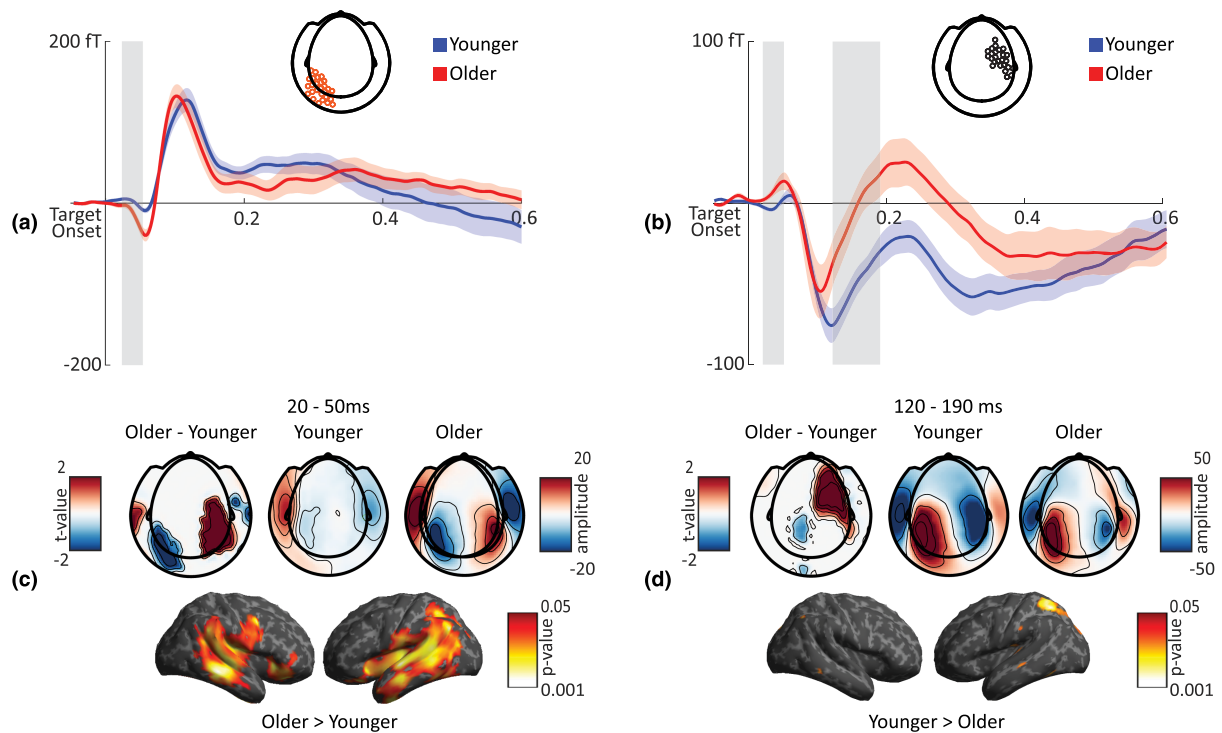

FIGURE 6 Group differences in target-related ERFs. (a) Grand average target-related ERFs (averaged over sensors highlighted in orange) for the older (red) and younger group (blue). Shaded areas denote between-participants standard error. Grey bars indicate significant differences between groups. (b) Same as (a) for sensors highlighted in black. (c) Top row: Topographies showing statistical distribution of these significant differences in addition to grand average topographies of ERFs within the time window highlighted in (a) (20–250 ms). Bottom row: *P*-value map (masked for *p* < 0.05, the whiter the lower) of the pattern of increased brain activation (source-reconstructed MEG data) in the older group. (d) Same as (d) but for the time window (120–190 ms)
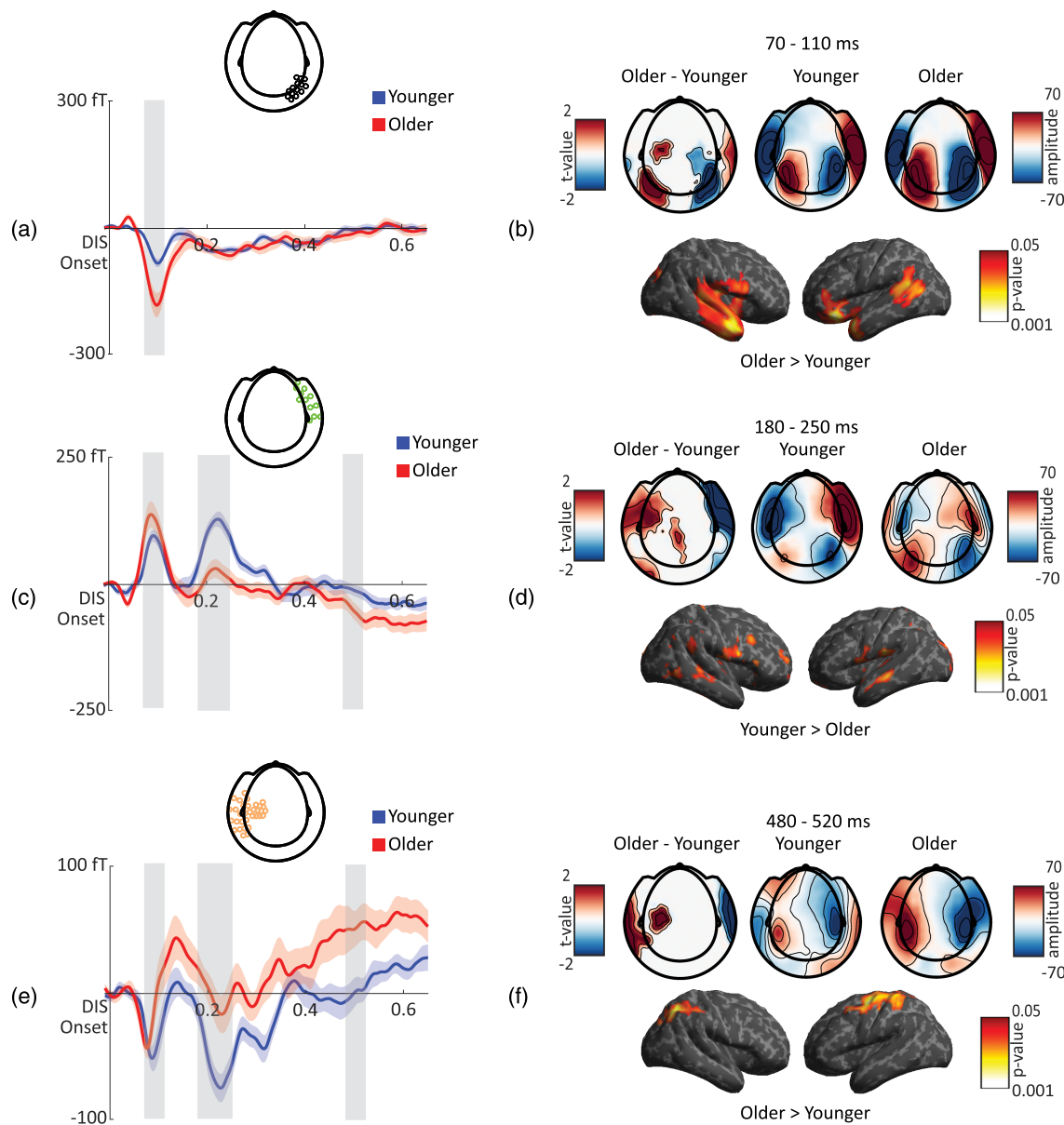
FIGURE 7 Group differences in early distracting sound-related ERFs. (a) Grand average DIS1-related ERFs (averaged over sensors highlighted in black) for the older (red) and younger group (blue). Shaded areas denote between-participants standard error. Grey bars indicate significant differences between groups. (b) Top row: Topographies showing statistical distribution of these significant differences in addition to grand average topographies of ERFs within the time window highlighted in (a) (70–110 ms). Bottom row: *P*-value map (masked for *p* < 0.05, the whiter the lower) of the pattern of increased brain activation (source-reconstructed MEG data) in the older group. (c) Same as (a) for sensors highlighted in green. (d) Same as (b) but for the time window (180–250 ms). (e) Same as (a) for sensors highlighted in orange. (f) Same as (b) but for the time window (480–520 ms)

previous studies (Curran et al., 2001; Erel & Levy, 2016; Greenwood et al., 1993; Olk & Kingstone, 2015), the groups did not differently benefit from the cue information to faster discriminate the target pitch (Figure 4), suggesting no major effect of age on top-down attentional orienting capacities, as observed at the behavioural level. It is important to note that the cueing effect was relatively weak in the present experiment (Figure S2) compared with previous studies (Nissen & Corkin, 1985; Tales et al., 2002), possibly due to the 1:1 ratio of informative and uninformative trials (Risko & Stolz, 2010).

4.1.1 | Target anticipation

Upon comparing cue-related fields between groups, we found that group differences lie within the CNV period. The CNV is thought to index top-down attention deployment and motor preparation in anticipation of an upcoming event (Bidet-Caulet et al., 2015; Brunia, 1999; Brunia & van Boxtel, 2001b; Gómez et al., 2004, 2007; Walter et al., 1964). It has been associated with the activation of a wide range of cortical and subcortical areas, including temporal, frontal and cingulate cortices, as well as supplementary motor areas (Chennu et al., 2013; Gómez et al., 2007).

In the present study, we have found inconclusive evidence regarding the brain location of the impact of ageing upon the magnetic counterpart of the CNV, the CMV. On the MEG sensor level, the pattern of results hints to differences around central regions, and the MEG source-level analysis revealed increased activation for the younger group in the postcentral and Heschl gyri. The focal localization of these effects precludes any strong claim on the brain location of the ageing effect on the CNV response.

4.1.2 | Target processing

For target-related fields, we found that older participants displayed a larger P50m and smaller N1m on its falling edge. Sources of the enhanced P50 with ageing are found centred in the superior temporal regions in the auditory cortices. This enhanced temporal P50 is in line with previous reports of enhanced early sensory components with ageing (Anderer et al., 1998; Dushanova & Christov, 2013; Gmehlin et al., 2011; Pelosi & Blumhardt, 1999) and has been accounted for by the inhibitory deficit hypothesis (Amenedo & Díaz, 1998; Knight et al., 1999). According to this hypothesis, enhancements of early sensory responses reflect a reduction in the capacity of the prefrontal cortex to exert its inhibitory modulation of thalamic inputs towards primary sensory cortices. Regarding the N1 amplitude, previous results have been conflicting with evidence that older participants display a reduced (e.g. Zanto et al., 2010) or an enhanced (e.g. Anderer et al., 1998; Gajewski et al., 2018) N1 response.

We also found a reduced target P3 in the older group in EEG data. A target-P3 or P3b reduction with ageing is a rather consistent finding across modalities (Chao & Knight, 1997; Gaeta et al., 2003; Karayanidis et al., 1995; Kok, 2000; Lorenzo-López et al., 2007; Woods, 1992) and has been interpreted as an age-related reduction in cognitive resources committed to stimulus processing (Tusch et al., 2017). We posit that differences between MEG and EEG data could be due to differences in these signals' sensitivity to source orientation, that is, MEG is insensitive to radially oriented sources (e.g. Ahlfors et al., 2010).

Indeed, the EEG topography of the target P3 or P3b is consistent with radial generators in the parietal regions (Halgren, 2009; Picton et al., 1999; Scherg et al., 1989; Shahin et al., 2007).

4.2 | Impact of ageing on distractor processing

In comparison with the younger group, older participants displayed a larger distraction cost in RTs. This increased susceptibility to task-irrelevant distractors is a recurrent finding in the literature using unisensory (visual or auditory) or multisensory paradigms (Bélanger et al., 2010; Gazzaley et al., 2005; Li & Zhao, 2015; Mevorach et al., 2016; Parmentier & Andrés, 2009).

4.2.1 | Enhanced sensory responses to distractor

In line with previous works (Chao & Knight, 1997; Gazzaley et al., 2005), the early evoked response to the distracting sounds around 100 ms (N1m) was found enhanced in the older group at the MEG sensor and source level, in the temporal cortices, which suggests enhanced sensory processing of the distracting sounds in the older group. This is also in keeping with the enhanced P50 in the elderly observed for the target in the current study (see Section 4.1.2).

4.2.2 | Reduced P3 complex to distractor

In addition, both at the EEG and MEG sensor levels, the older group displayed reduced early components of the P3 complex (also known as the P3a) to distracting sounds, in agreement with previous results (Bertoli & Bodmer, 2016; Friedman et al., 1998; Friedman & Simpson, 1994; Knight, 1987; Morrison et al., 2019; Tusch et al., 2017). The late component of the P3 complex was also found reduced in the older group at the EEG sensor level, in agreement with previous reports on the effect of ageing on the P3b (Fjell et al., 2007; O'Connell et al., 2012; Polich, 1997; Porcaro et al., 2019; Walhovd & Fjell, 2001; Wronka et al., 2012), in keeping with the results observed here for the target P3b (see Section 4.1.2).

In our study, the sources of those ageing-related reductions are distributed with local temporal, parietal and prefrontal maxima. The P3a has been shown to be generated in a large network that includes prefrontal, cingulate, temporoparietal and hippocampal areas (Barry et al., 2019; Dien et al., 2003).

The P3 complex is a non-unitary complex signal that has been associated to different steps of the orienting response (e.g. Escera et al., 1998; Polich & Criado, 2006).

Following this interpretation, a reduced P3 complex would suggest a reduced orienting response and distraction effect, which is contradictory to the larger distraction cost in RTs observed in the older group. Such a discrepancy between changes in P3a and behavioural distraction has already been observed in other populations, such as children with ADHD (Gumenyuk et al., 2005).

Another interesting hypothesis concerning the functional role of the P3 complex (or P300) is the implication of inhibitory brain mechanisms (Polich, 2007). More precisely, the P300 could reflect the inhibition of neural activity to facilitate information transmission from frontal (P3a) to temporoparietal (P3b) regions (Polich, 2007). According to this hypothesis, a reduction in the P3 complex amplitude in older participants could reflect a reduction in the ability to rapidly process and inhibit task-irrelevant information, in line with the inhibitory deficit hypothesis of ageing (Hasher & Zacks, 1988).

4.2.3 | Altered RON to distractor

In response to distracting sounds, the older group displayed an increased RON both at the EEG and MEG sensor levels. MEG source analysis revealed a larger activation of parietal cortex and motor areas during the RONm. The RON has been proposed to index the reallocation of attention and cognitive resources from task-irrelevant events back towards the primary task (Berti, 2008; SanMiguel et al., 2008; Schröger & Wolff, 1998) and/or additional post-stimulus evaluation process (Berti, 2008). The alteration of the RON with ageing has been previously reported (Getzmann et al., 2013; Horváth et al., 2009b; Mager et al., 2005; Tusch et al., 2017) with evidence that the RON could explain in part ageing-related deterioration in behavioural performances (Getzmann et al., 2015). We posit that the increased RON would reflect a prolonged reorientation process towards the task at hand, as a consequence of the exacerbated processing of distracting sounds. Indeed, both enhanced bottom-up processing of distractors (enhanced N1m) and reduced inhibitory processes (reduced P3 complex and reduced activation of the left dorsolateral prefrontal cortex in the gamma band) (ElShafei et al., 2020) have been observed.

To our knowledge, the present study is the first to identify the potential brain correlates of the age-related effect on the RON within the parietal cortex and motor areas. Thus, the prolonged reorientation process would be subtended by the posterior nodes of the top-down dorsal attentional network (Corbetta & Shulman, 2002).

4.3 | CONCLUSION: TOP-DOWN/ BOTTOM-UP BALANCE IN AGEING

To sum up results obtained using the CAT (present study and ElShafei et al., 2020), older populations present reduced inhibition (reduced alpha power) of irrelevant information during target expectancy and reduced allocation of cognitive resources during target expectancy (reduced CMV) and to relevant stimuli (smaller target P3). Moreover, in response to unexpected sounds, older persons present enhanced early processing of distractors (enhanced N1m), reduced recruitment of inhibitory brain mechanisms (reduced P3 complex), reduced inhibitory signal from the left dorsolateral PFC (reduced gamma activity) and a prolonged reorientation towards the task (larger RONm and RON), in line with an enhanced distraction cost in RTs. Taken together, these results speak for a deficit in top-down inhibitory processes present at several stages of the attention selection in ageing, resulting in enhanced distractibility at the behavioural level.

CONFLICT OF INTEREST
The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

AUTHOR CONTRIBUTIONS
Hesham A. ElShafei: Conceptualization, methodology, investigation, data curation, data analysis, visualization, writing—original draft preparation. **Rémy Masson:** Investigation, data analysis, visualization. **Camille Fakche:** Data curation, investigation, data analysis, visualization. **Lesly Fornoni:** Investigation, data curation. **Annie Moulin:** Writing—reviewing and editing. **Anne Caclin:** Data analysis, visualization, writing—reviewing and editing. **Aurélie Bidet-Caulet:** Project administration and funding acquisition, conceptualization, methodology, visualization, writing—reviewing and editing, supervision.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

In accordance with the French legislation (Loi Huriet-Serusclat) in force at the time of registration, the participants only consented that the data can be used to meet the objectives set in this study by the research team. Therefore, in accordance with good clinical practice, these data may not be used in any other context and may not be shared.

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