TITLE PAGE

TITLE: Not Just A Number: Age-Related Modulations of Oscillatory Patterns Underlying Top-Down and Bottom-Up Attention.

ABBREVIATED TITLE: Oscillatory patterns of attentional ageing

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Abstract

Attention operates through top-down (TD) and bottom-up (BU) mechanisms. Recently, it has been suggested that these mechanisms are supported by distinct frequency bands with slower (alpha) frequencies indexing facilitatory and suppressive mechanisms of TD attention and faster (gamma) frequencies indexing BU attentional capture. Ageing is characterized by increased behavioral distractibility, which can result from either a reduced efficiency of TD attention, or an enhanced triggering of BU attention. However, only few studies have investigated the impact of ageing on the balance between TD and BU attention and its oscillatory correlates. MEG data were collected from 14 elderly (mean age = 67) and 14 matched young (mean age = 25) healthy human participants while performing a modified version of the Competitive Attention Task with pitch discrimination. TD attention was manipulated by a visual cue that was either informative or not of the side of the monaural target sound. BU attention was triggered by binaural distracting sounds that were played (25% of trials) between the cue and the target. Behaviorally, older participants displayed an exacerbated distractibility to late distractors. Electrophysiologically, in comparison to young participants, they exhibited (1) deficits in the suppressive mechanisms of TD attention, indexed by a reduced alpha synchronization in task-irrelevant visual regions, (2) less prominent alpha peak-frequency differences between cortical regions, (3) a similar BU system activation indexed by distractor-induced gamma responses, and (4) a reduced activation of prefrontal inhibitory control regions. These results show that the ageing-related increased distractibility is of TD origin.

Significance Statement

We investigated the impact of ageing on top-down (TD) and bottom-up (BU) attention mechanisms as indexed by oscillatory activity in the alpha and gamma bands, respectively. Magnetoencephalographic data were collected in elderly and young participants performing a task engaging both TD and BU attention. Suppressive mechanisms of TD attention (indexed by alpha synchronization in task-irrelevant regions) but not facilitatory mechanisms (indexed by alpha desynchronization in task relevant regions) were found reduced with ageing. In addition, BU activation to distracting sounds (indexed by gamma synchronization) was unaffected; while TD control of this activation declined, with ageing. To our knowledge, this is the first demonstration of the TD origin of the ageing-related increased distractibility investigating brain oscillatory activities.

1 Introduction

Ageing is characterized by attentional difficulties, in particular a reduced capability to inhibit irrelevant information (Guerreiro et al., 2010; Zanto and Gazzaley, 2014). This exacerbated distractibility has been attributed to a degradation of inhibitory mechanisms (inhibitory deficit hypothesis, Hasher and Zacks, 1988) and a deterioration in the functioning of the frontal lobe (frontal aging hypothesis, West, 1996).

Attention operates through top-down (TD) and bottom-up (BU) mechanisms (James, 1890; Corbetta and Shulman, 2002). TD processes promote the processing of relevant stimuli through facilitatory and suppressive mechanisms, resulting in enhanced processing of relevant information and reduced brain responses to unattended inputs, respectively (review in Hillyard et al., 1998). Attention can also be oriented in a BU fashion towards task-irrelevant unexpected salient stimuli (Corbetta et al., 2000). A good balance between BU and TD mechanisms is thus crucial: enhanced distractibility can result from either a reduced efficiency of TD mechanisms, or an enhanced triggering of BU attentional capture. TD and BU processes are supported by partially segregated networks: (1) a dorsal fronto-parietal network, including the intraparietal sulcus and the frontal eye fields: and (2) a ventral fronto-parietal network, including the temporo-parietal junction and the ventral frontal cortex, respectively. The two networks mainly overlap in the lateral prefrontal cortex (Corbetta and Shulman, 2002; Corbetta et al., 2008). Recently, it has been suggested that signals in these networks are propagated via distinct frequency bands with slower frequencies supporting interactions along the TD network and faster) frequencies supporting communication in the BU network (Buschman and Miller, 2007).

Alpha oscillations (8–14 Hz) have been proposed to play a crucial role in TD anticipatory attention (review in Foxe and Snyder, 2011; Frey et al., 2015). More precisely, they play an active inhibitory role (Klimesch et al., 2007; Jensen and Mazaheri, 2010): reduced and enhanced alpha power reflect increased and decreased cortical excitability in task relevant and irrelevant areas, respectively (e.g. Kelly et al., 2006; Gomez-Ramirez et al., 2011; Weisz et al., 2011). Therefore, alpha rhythm is a suitable candidate for supporting facilitatory and suppressive mechanisms of anticipatory attention (ElShafei et al., 2018a). With ageing, TD attentional facilitatory processes, as indexed by alpha desynchronization, has been found to be either reduced (Deiber et al., 2013; Hong et al., 2015; van der Waal et

al., 2017), preserved (Leenders et al., 2018) or even enhanced (Heideman et al., 2018). However, TD suppressive processes indexed by alpha synchronization seem to deteriorate (Vaden et al., 2012).

Gamma oscillations (>30 Hz) have also been associated with attention (review in Fries, 2009) with evidence suggesting that BU feedforward signaling propagates predominantly via these oscillations in primate sensory areas (Bastos et al., 2015; Michalareas et al., 2016). Moreover, gamma activity has been found in frontal regions of the ventral network in response to novel sounds (e.g. Lee et al., 2007; Akimoto et al., 2013). To our knowledge, no study has investigated the impact of ageing on gamma oscillatory activity supporting BU attention. In addition, no study has tackled how ageing would impact the balance between TD and BU mechanisms of attention, supported by activity in different oscillatory bands.

Therefore, the aim of the present study was to characterize the brain origins of the exacerbated distractibility in elderly by investigating the impact of ageing on oscillatory activities supporting the balance between TD and BU attention. For this purpose, we recorded MEG activity from young and elderly participants while performing the Competitive Attention Task (Bidet-Caulet et al., 2014), a novel paradigm that permits the assessment of BU and TD mechanisms of auditory attention and the interaction between them.

We hypothesized that ageing would be characterized by an (1) exacerbated behavioral distractibility, (2) reduced TD filtering of irrelevant information, indexed by alterations in the alpha band, and (3) impaired gamma responses to distracting sounds and/or impaired modulation of these responses by TD attention.

2 Material & METHODS

2.1. Participants

Participants were 14 young (mean age = 25 ± 0.67 Standard Error of Mean (SEM); range: 20—29 years; 5 females) and 14 elderly (mean age = 67 ± 1.08 SEM; range: 61—75 years; 5 females) adults. The two groups were matched for sex, handedness, scholar and musical education (see Table 1). As expected, the 2 groups significantly differ in age (non-paired t-test $p < 0.001$) but did not significantly differ in scholar (non-paired t -test $p = 0.67$) and musical (non-paired t -test $p = 0.32$) 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. The study was approved by the local ethical committee, and subjects gave written informed consent, according to the Declaration of Helsinki, and they were paid for their participation. Please note that data from all young participants are included in the analysis presented in a previous study of gamma activity in young adults (ElShafei et al., 2018b).

	Elderly group	***Young Group***
Age (years ± SEM)	67 ± 1.08	25 ± 0.67
Gender	5F, 8M	5F, 8M
Handedness	14R	14R
Scholar Education (years ± SEM)	15 ± 0.71	15 ± 0.57
Musical Education (years ± SEM)	1 ± 0.45	2 ± 0.68

Table1. Group demographics. SEM, standard error of the mean; F, Female; M, Male; R, right-handed.

2.2. Stimuli and tasks

2.2.1. Competitive Attention Task (CAT)

In 75 % of the trials, a target sound (100 ms duration) followed a central visual cue (200 ms duration) with a fixed delay of 1000 ms (see Figure 1). The cue was a green arrow, presented on a grey-background screen, pointing either to the left, right, or both sides. Target sounds were monaural pure tones (carrier frequency between 512 and 575 Hz; 5 ms rise-time, 5 ms fall-time). In the other 25 %, 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 ms to 350 ms after the cue offset were classified as DIS1, those with a distracting sound played from 350 ms to 650 ms after the cue offset were classified as DIS2, those with no distracting sound were classified as NoDIS. A total of 40 different ringing sounds were used as distracting sounds (clock-alarm, door-bell, phone ring, etc.) for each participant.

The cue and target categories were manipulated in the same proportion for trials with and without 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 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*, 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 category (informative, uninformative) and distractor condition (DIS1 or DIS2). Each distracting sound was thus played 4 times during the whole experiment, but no more than once during each 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 capacities, the pitch difference between the two target sounds was defined in a Discrimination Task (see below). Participants were informed that informative cues were 100 % predictive 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 3.4 second response window. In the absence of the visual cue, a blue fixation cross was presented at the center of the screen. Subjects were instructed to keep their eyes fixated on the cross.

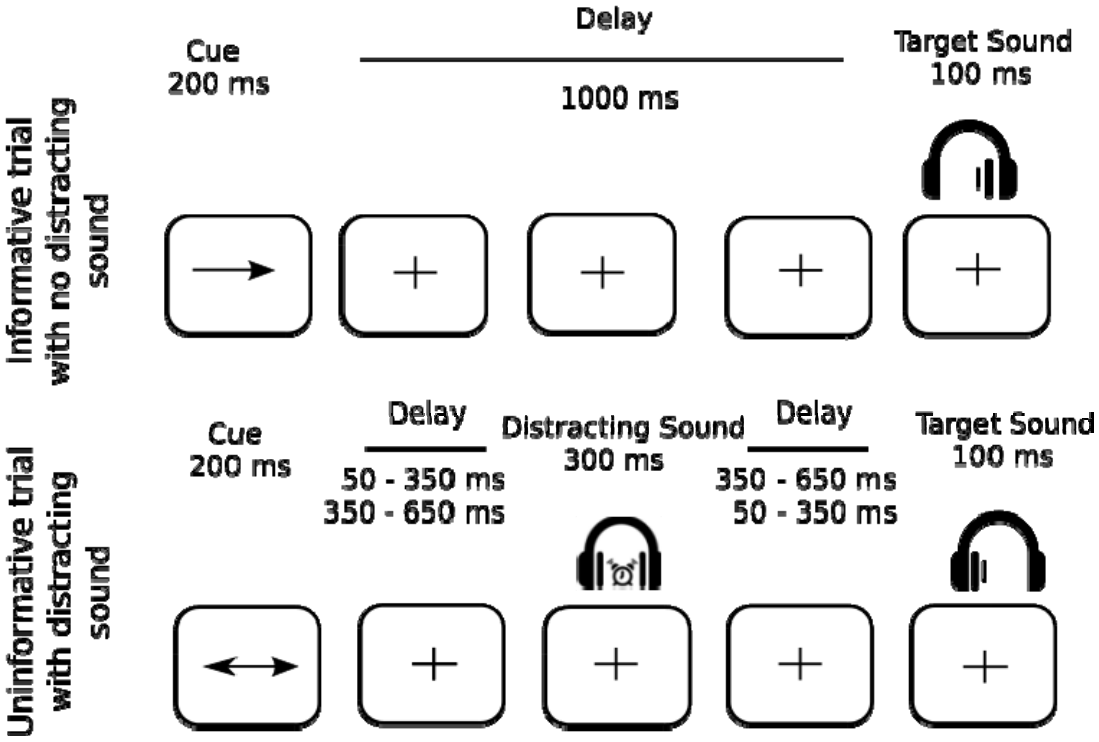

Figure 1. Protocol. Top row. Example of an informative trial with no distracting sound: a one-sided visual cue (200 ms duration) indicated in which ear (left or right) the target sound would be played (100 ms duration) after a fixed 1000-ms delay. Bottom row. Example of an uninformative trial with a distracting sound: a two-sided visual cue (200 ms duration) did not provide any indication in which ear (left or right) the target sound will be played. In 25 % of the trials, a binaural distracting sound (300 ms duration), such as a clock ring, was played during the delay between cue and target. The distracting sound could equiprobably onset in two different time periods after the cue offset: in the 50–350 ms range, or in the 350–650 ms range.

2.2.2. Discrimination Task

Participants were randomly presented with one of two target sounds: a low-pitched sound (512 Hz) and a high-pitched sound (575 Hz; two semitones higher), equiprobably in each ear (four trials per ear and per pitch). As described above, participants were asked to categorize the target sounds as either high- or low-pitched sound within 3 seconds.

2.2.3. 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 threshold was determined for the two target sounds differing by 2 semitones (512 and 575 Hz), for each ear, for each participant using the Bekesy tracking method (Von Békésy and Wever, 1960). The target sounds were then presented at 25 dB sensation level (between 30 and 69.5 dB A in old, and between 37.5 and 50.75 dB A in young participants) while the distracting sounds were played at 55 dB sensation level (between 40 and 79.5 dB A in old, and between 47.5 and 60.75 dB A in young participants), above the target sound thresholds. Second, participants performed the discrimination task. 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 3 semitones between the two targets (auditory thresholds were then measured with the new targets). Afterwards, participants were trained with a short sequence of the Competitive Attention Task. Finally, MEG and EEG were recorded while subjects performed 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 minutes. After the MEG/EEG session, participants' subjective reports regarding their strategies were collected.

2.3. Behavioral Data Analysis

For behavioral data analysis, a button press before target onset was considered as a false alarm (FA). A trial with no button-press after target onset and before the next cue onset was considered as a miss trial. A trial with no FA and with a button-press after target onset was counted as correct if the pressed button matched the response mapped to the target sound, and as incorrect if otherwise. Reaction-times (RTs) to targets were analyzed in the correct trials only. The influence of (1) age group (2 levels: young and elderly), (2) cue condition (2 levels: informative and uninformative), and (3) distractor condition (3 levels: NoDis, DIS1 and DIS2) on percentage of incorrect responses and median reaction times (RTs) of correct responses was tested using a linear mixed-effects models (lme4 package, Bates et al., 2014 for R Team, 2014). A random effect was included for each participant, allowing us to model variability between participants. For post-hoc analysis we used the Lsmean package (Lsmean version 2.20-23; Searle et al., 1980) where p-values were considered as significant at $p<0.05$ and adjusted for the number of comparisons performed (Tukey method).

Moreover, planned analyses of the CUE BENEFIT were carried out between groups on the differences in RTs Uninformative NoDIS – Informative NoDIS and of distractor effects on the differences in RTs NoDIS – DIS1 (as a measure of the AROUSAL BENEFIT) or DIS2 – DIS1 (as a measure of ATENTION CAPTURE COST), using non-paired t-tests (Bidet-Caulet et al. 2014; Masson and Bidet-Caulet 2018).

2.4. Brain Recordings

Simultaneous EEG and MEG data were recorded, although the EEG data will not be presented here. The MEG data were acquired with a 275-sensor axial gradiometer system (CTF Systems Inc., Port Coquitlam, Canada) with continuous sampling at a rate of 600Hz, a 0–150Hz filter bandwidth, and first-order spatial gradient noise cancellation. Moreover, eye-related movements were measured using vertical and horizontal EOG electrodes. Head position relative to the gradiometer array was acquired continuously using coils positioned at three fiducial points; nasion, left and right pre-auricular points. Head position was checked at the beginning of each block to control head movements.

In addition to the MEG/EEG recordings, T1-weighted three-dimensional anatomical images were acquired for each participant using a 3T Siemens Magnetom whole-body

scanner (Erlangen, Germany). These images were used for reconstruction of individual head shapes to create forward models for the source reconstruction procedures. The processing of these images was carried out using CTF's software (CTF Systems Inc., Port Coquitlam, Canada). MEG data were pre-processed in the sensor space using the software package for electrophysiological analysis (ELAN pack; Aguera et al., 2011) Further analyses were performed using Fieldtrip (Oostenveld et al., 2011), an open source toolbox for MATLAB and custom-written functions. Behavioral analysis were carried out using R (Team, 2014)

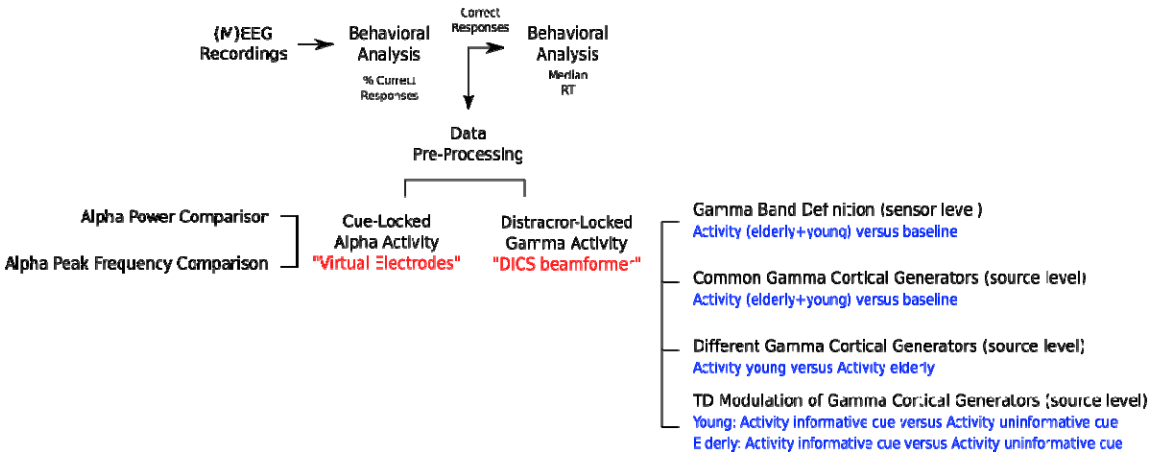

Figure 2. Outline of the analysis pipeline.

2.5. Data Pre-processing (Figure 2)

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 muscular activity or sensor jumps were excluded semi-manually using a threshold of 2200 and 10000 femtoTesla respectively. For all participants, more than 75 % of trials remained after rejection for further analyses. Independent component analysis was applied on the band-pass filtered (0.1-40Hz) data in order to remove eye-related (blink and saccades) and heart-related artefacts. Subsequently, components (four on average) were removed from the non-filtered data via the inverse ICA transformation. Data were further notch filtered at 50, 100 and 150Hz and high-pass filtered at 0.2Hz.

2.6. Cue-Related Alpha Activity (Distractor-Free Trials)

Region of interests, time-window and frequency bands for the analysis of cue-related alpha activity was based on previous results in young healthy adults obtained using a similar paradigm (ElShafei et al., 2018a).

2.6.1. Virtual-Electrode Level Analysis and Defining ROIs

The source space was subdivided into 69 anatomically defined brain parcels according to the Talairach Tournoux atlas (Talairach and Tournoux, 1988; Lancaster et al., 1997). Broadmann areas 17, 18 and 19 were defined as the visual regions of interest (ROIs) while areas 22, 41 and 42 were defined as the auditory ROIs and areas 4 and 6 were defined as the motor ROIs, in each hemisphere.

2.6.2. Reconstruction of Source Activity

In order to reconstruct activity at the source level, we computed the time-frequency signal of the ROIs defined above at the virtual electrode level. Using the linearly constrained minimum variance (LCMV) beamformer (Van Veen et al., 1997) beamformer, spatial filters were constructed from the covariance matrix of the averaged single trials at sensor level (-0.8 – 2s, relative to cue onset, 1-20 Hz, lambda 5%) and the respective leadfield. Spatial filters were multiplied by the sensor level data in order to obtain the time course activity at each voxel of interest.

Activity was averaged across all voxels within each ROI in both hemispheres. Thus, limiting our analysis to three ROIs (one auditory, one visual and one motor). For each ROI, the evoked potential (i.e., the signal averaged across all trials) was subtracted from each trial. Subsequently, the oscillatory power, of distractor-free trials, was calculated using Morlet Wavelet decomposition with a width of four cycles per wavelet (m=7; Tallon-Baudry and Bertrand, 1999) at center frequencies between 5 and 18 Hz, in steps of 1 Hz and 50 ms.

2.6.3. Impact of Age on Alpha Activity: Power differences

In order to investigate differences between groups in low and high alpha sub-bands, baseline-corrected (-0.6 to -0.2s pre-cue) alpha power (computed using Morlet Wavelets) was averaged between 7 and 11Hz, and between 11 and 15Hz, separately, in each ROI. Subsequently, alpha activity (0.6 to 1s post-cue by step of 50 ms) within each alpha sub-band

was contrasted between groups using a non-parametric cluster-based permutation analysis (Maris and Oostenveld, 2007). Please note, that for this test, cluster-based permutations control for multiple comparisons in the time dimension.

2.6.4. Impact of Age on Alpha Activity: Alpha Peak Frequency

Alpha power (computed using Morlet Wavelets) was averaged between 0.6 and 1s for each ROI, to extract the power spectrum in each subject. Afterwards, individual alpha peak frequency (iAPF) was defined separately for each ROI, in each subject. For auditory and motor ROIs, the peak was defined as the frequency with the maximum alpha power decrease relative to the *baseline* (-0.6 to -0.2s pre-cue onset) between 5 and 15 Hz. For visual virtual electrodes, the peak was defined as the frequency with the maximum alpha power increase relative to the baseline.

The iAPFs were fit into a linear mixed-effects model (lme) with the following factors as fixed effect: (1) age group (2 levels: young and elderly), (2) ROI (3 levels: auditory, visual and motor). A random effect was included for each participant, allowing us to model variability between participants. Similarly to previous analysis, for post-hoc analysis, we used the Lsmean package.

2.7. Distractor-Related Gamma Activity

2.7.1. Gamma Band (Sensor level): Definition

This analysis was done to define the time-frequency range of gamma activity of interest. First, for each distractor onset time-range, we have created surrogate distractors in the NoDIS trials with similar distribution over time than the real distractors. Afterwards, the oscillatory power, of distractor and (surrogate distractor) trials was calculated using Morlet Wavelet decomposition with a width of four cycles per wavelet (m=7; Tallon-Baudry and Bertrand, 1999) at center frequencies between 40 and 150 Hz, in steps of 1 Hz and 10 ms. Data from both groups were pooled together and activity of interest (defined between 0 and 0.35s post-distractor onset and 50-110Hz) was contrasted between distractor and surrogate trials using a nonparametric cluster-based permutation analysis (Maris and Oostenveld, 2007). This contrast extracts distractor-related activity clear of cue-related activity.

2.7.2. Gamma Band (Source level): Computation

In order to estimate the brain regions driving the sensor-level distractor-related gamma activity (0.1-0.3 s post-distractor onset, 60 to 100Hz), we have utilized the frequency–domain adaptive spatial technique of dynamical imaging of coherent sources (DICS; Gross et al., 2001).

Data, from both surrogate and real distractors were concatenated, and cross-spectral density (CSD) matrix (-**0.2 to 0.6 s**, relative to real/surrogate distractor onset) were calculated using the multitaper method with a target frequency of **80 (±30) Hz.** For each participant, an anatomically realistic single-shell headmodel based on the cortical surface was generated from individual head shapes (Nolte, 2003). A grid with 0.5 cm resolution was normalized on an MNI template, and then morphed into the brain volume of each participant. Leadfields for all grid points along with the CSD matrix were used to compute a common spatial filter that was used to estimate the spatial distribution of power for time-frequency windows of interest.

2.7.3. Gamma Power Source Level Analysis

For each participant, we estimated source-level activity (0.1-0.3 s post-distractor onset, 60 to 100Hz) for each cue category (informative and uninformative) and for both cue categories concatenated. We performed three analyses:

(1) To characterize the brain areas activated in the gamma band during the distracting sound presentation, data from both groups were pooled together and distractor-related gamma activity was contrasted to surrogate distractor-related gamma activity.

(2) To investigate group differences in distracting sound processing in the gamma band, surrogate-corrected gamma activity (surrogate distractor-related gamma activity was subtracted from distractor-related gamma activity) was compared between groups.

(3) To investigate a potential interaction between groups and the use of the cue information, for each group separately, surrogate-corrected gamma activity in the informative cue condition was contrasted to surrogate-corrected gamma activity in the uninformative cue condition.

All tests have been carried out using non-parametric cluster-based permutation analysis (Maris and Oostenveld, 2007). Please note, that for these tests, cluster-based permutations control for multiple comparisons in the source space dimension.

3 Results

3.1 Behavioral Analysis

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 %). In order to investigate behavioral performances (percentage of incorrect responses and RTs), a lme model was used with 3 factors: (1) age group (2 levels: young and elderly), (2) cue condition (2 levels: informative and uninformative), and (3) distractor condition (3 levels: NoDis, DIS1 and DIS2).

2.7.4. Behavioral Analysis: Incorrect Response Percentage (Figure 3)

Only a significant main effect of the distractor condition ($F(2, 52) = 8.9$, $p < 0.01$, $\eta^2 = 0.21$) was found on the percentage of incorrect responses, with no main effect of group ($F(1, 15) = 2.1$, $p = 0.15$, $\eta2 = 0.07$). Post-hoc tests indicated that participants, from both groups, committed more errors in the late DIS2 condition in comparison to the early DIS1 ($p < 0.01$) and the NoDIS ($p < 0.001$) conditions.

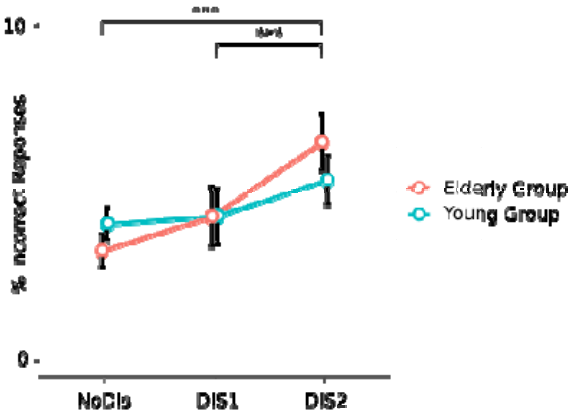

Figure 3. Percentage of Incorrect Responses averaged across cue conditions, according to distractor conditions, for both groups. *** $P < 0.001$. Error bars represent SEM.

2.7.5. Behavioral Analysis: Median Reaction Times (Figure 4)

A main effect of cue category ($F(1, 26) = 3.7$, $p < 0.01$, $\eta^2 = 0.22$) was found on reaction times. Participants were faster when the cue was informative in comparison to the

uninformative cue. In addition we found a main effect of the distractor condition ($F(2, 52) = 95.2$, $p < 0.01$, $\eta^2 = 0.64$). Post-hoc tests indicated that in comparison to the NoDIS condition, participants were faster in the early DIS1 condition ($p < 0.001$) but slower in the late DIS2 condition ($p<0.001$). In addition, participants were faster in the early DIS1 than in the late DIS2 condition ($p<0.01$). Most interestingly, we found a significant interaction between age and distractor factors ($F(2, 52) = 10.9$, $p < 0.01$, $\eta^2 = 0.17$). Post-hoc tests indicated that elderly participants were slower than the young ones in the late DIS2 condition ($p= 0.04$).

Unpaired t-test between groups confirmed that the attention capture effect (DIS2 – DIS1) was significantly more pronounced for the elderly group ($p < 0.01$); whereas the arousal facilitation effect (NoDIS – DIS1; $p = 0.29$) and the cue benefit effect (Uninformative NoDIS – Informative NoDIS; $p = 0.83$) were not significantly different between groups.

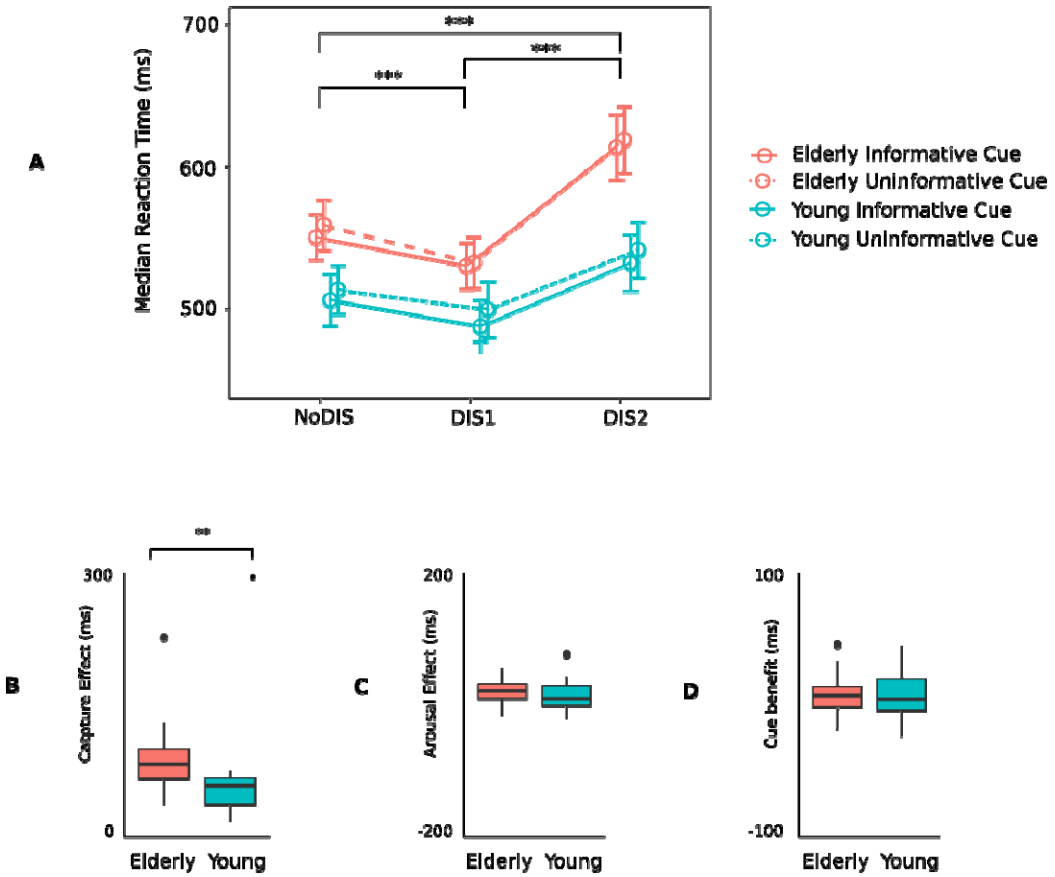

Figure 4. (A). Median RTs in each group according to cue information and distractor conditions. Error bars represent SEM. Boxplot of the Attention capture effect (B), the Arousal effect (C), and the Cue benefit effect (D), for each group. ** $P < 0.01$.

3.2 Cue-related Alpha Analysis

3.2.1 Ageing and Alpha Power Modulations (source level)

Upon contrasting post-cue activity between both groups in each ROI (motor, auditory or visual), no differences were found in the low alpha sub-band (7-11 Hz). However, in the high alpha sub-band (11-15 Hz), we found two significant positive clusters: one in the visual ROI ($p = 0.02$) and another in the motor ROI ($p = 0.01$). In the visual ROI, as shown in Figure 5, alpha power was significantly lower (less alpha synchronization) in the elderly than in the young participants between 600 ms and 1000 ms. In the motor ROI, the elderly displayed lower alpha power (more alpha desynchronization) than young participants between 600 ms and 800 ms.

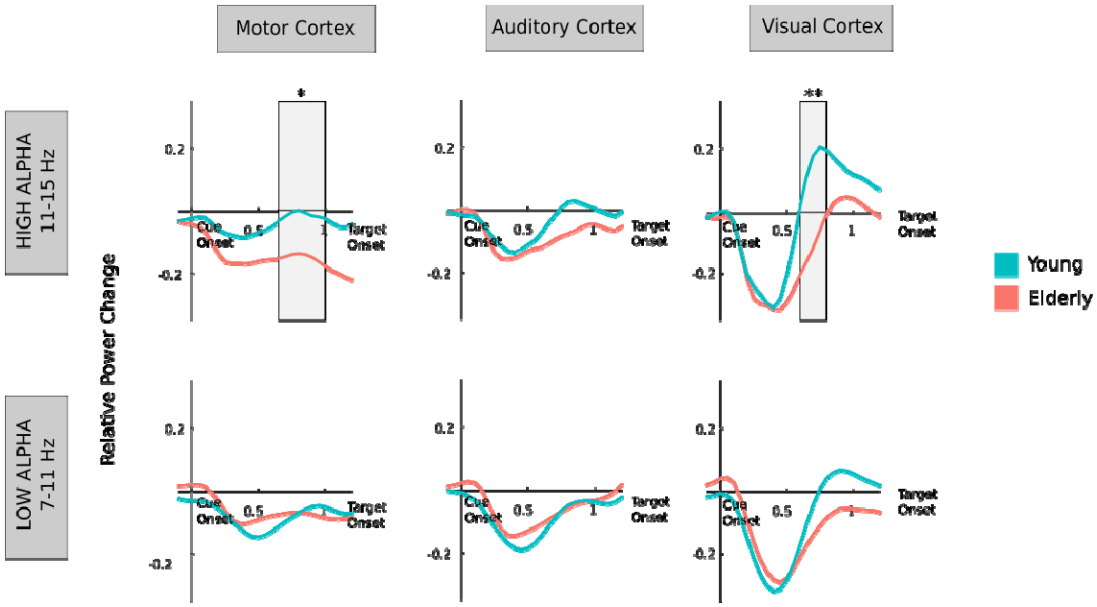

Figure 5. Time-course of alpha activity averaged between 7-11Hz and 11-15Hz across virtual ROIs. Grey Rectangles represent time-windows of significant group differences based upon cluster-based permutation testing. * $p < 0.05$.

2.7.6. Ageing and Alpha peak frequency (source level)

In order to investigate the alpha peak frequency in virtual ROIs, a lme model was used with 2 factors: (1) age (2 levels: young and elderly), and (2) ROI (3 levels: auditory, visual and motor). The lme model yielded a significant interaction between age and ROI ($F(2,52) = 4.1$, $p < 0.01$, $\eta^2 = 0.11$). Post-hoc tests indicated that, only in the young group, the alpha peak

frequency was significantly higher in the visual ROI (mean = 12.32 Hz ± 0.44 SEM) than in the auditory (mean = 9.39 Hz ± 0.58 SEM) and the motor ROIs (mean = 10 Hz ± 0.58 SEM) ($p < 0.001$ and $p = 0.01$, respectively), as shown in Figure 6.

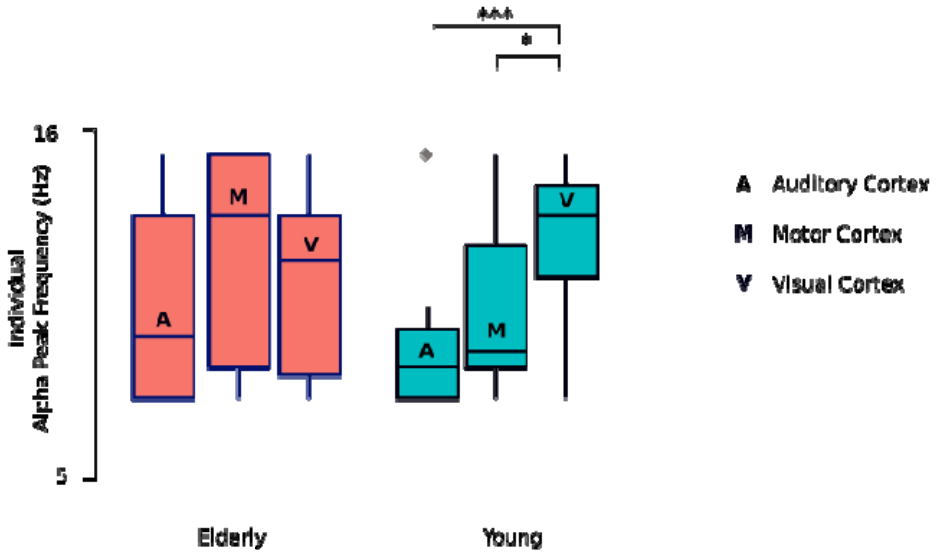

Figure 6. Individual Alpha Peak Frequency in each virtual ROIs for each group. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Error bars represent SEM.

3.3 Distractor-Related Gamma Activity

3.3.1 Gamma-band definition (sensor level)

Oscillatory data were pooled from both groups and real-distractor high-frequency activity was contrasted to that of surrogate-distractor using non-parametric cluster-based permutation testing. As shown in Figure 7, this contrast revealed one significant positive cluster (p = 0.001) indicating an increase in gamma activity centered spatially around left and right temporal sensors (Fig 7A), temporally between 0.1 and 0.3s post-distractor onset (Fig 7B & C), and frequency-wise between 60 and 100 Hz (Fig 7B & D).

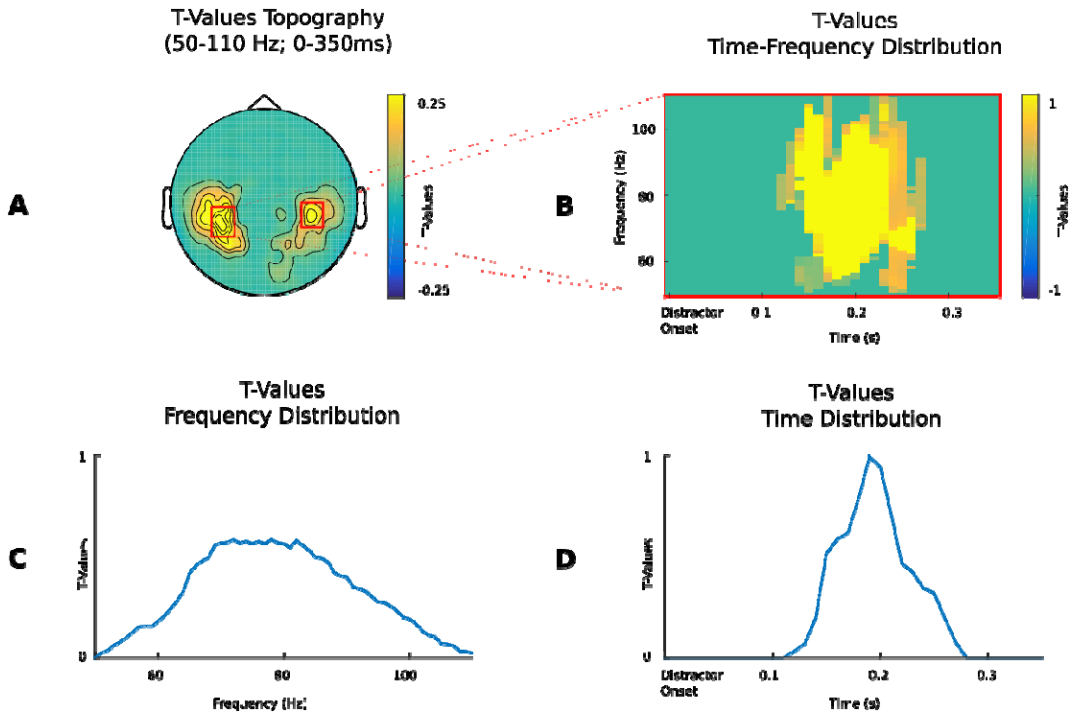

Figure 7. Common sensor level gamma activity to distractor. A. Topographical maps averaged between 50-110 Hz and 0-0.35 seconds post-distractor onset, of the t-values, masked at $p < 0.05$ of the contrast between distractor and surrogate distractor gamma activity. **B.** Time-frequency representations of t-values (of the aforementioned test) of the sensors highlighted by red boxes in A. **C.** Frequency distribution of t-values of the aforementioned sensors averaged across the time dimension. **D.** Time distribution of t-values of the aforementioned sensors averaged across the frequency dimension.

3.3.2 Gamma Activity: Common Activation (source level)

Based upon sensor level results, we have computed DICS beamformer sources for each participant between 60-100Hz and 0.1-0.3s post-distractor. Once again, source-level data was pooled from both groups and real-distractor gamma activity was contrasted to that of surrogate distractors using non-parametric cluster-based permutation testing.

The aim of this test was to highlight the brain regions that are commonly activated in both groups in the gamma band. A significant positive cluster ($p < 0.01$) indicating a bilateral increase in gamma activity notably in (1) the auditory cortices, and (2) the tempo-parietal junctions and the ventro-lateral prefrontal cortices (Figure 8). Other regions included the middle and posterior cingulate gyri, pre- and post-central gyri, the Precuneus, and the inferior temporal gyri.

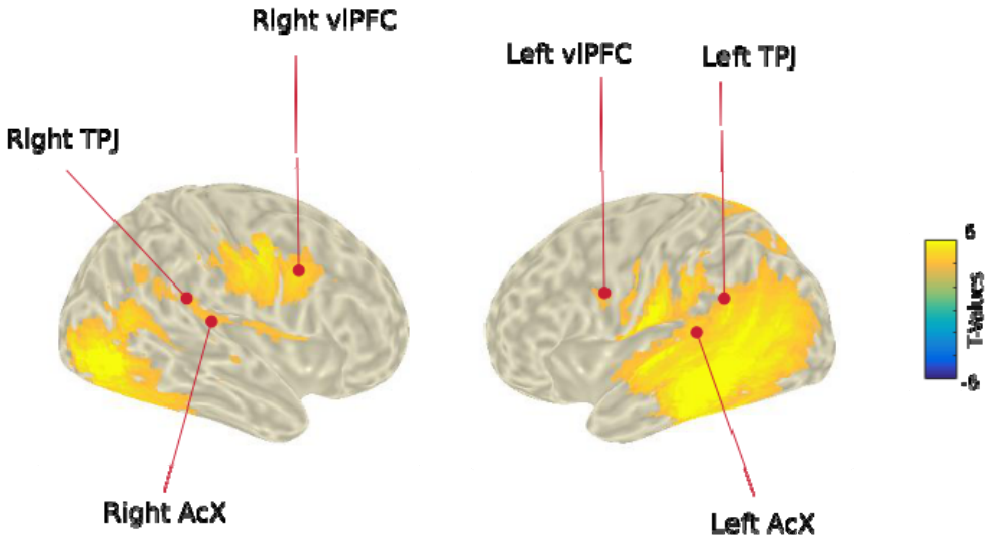

Figure 8. Common source level gamma activity to distractor. Distributions of T-values, masked at *p<0.05*, from Cluster Based Permutation tests contrasting real and surrogate distractor gamma activity (60-100Hz and 0.1-0.3 post-distractor) pooled from both groups at the source level. AcX: Auditory Cortex. TPJ: temporo-parietal junction. vlPFC: ventro-lateral prefrontal cortex.

2.7.7. Gamma Activity: Group Comparison (source level)

The aim of this test was to highlight the brain regions that are differentially activated in the elderly and young groups, in the gamma band. For each participant, real distractor source-

level data (60-100 Hz, 0.1-0.3s) were corrected by subtracting surrogate-distractor activity. Corrected distractor gamma activity was contrasted between groups using non-parametric cluster-based permutation testing. A significant positive cluster ($p = 0.01$) was found notably in (1) the left dorso- and ventro-medial prefrontal cortices, and (2) the left anterior cingulate gyrus (Figure 9A). Other regions included the left pre- and post- central gyri, the left supplementary motor area, the left superior parietal lobule. All these regions displayed a higher gamma activation for the young group compared to the elderly group.

3.3.3 Gamma Activity: Modulation by Cue Information

To investigate the effect of top-down attention on bottom-up processing, we analyzed the effect of cue information on the gamma response to distracting sounds, in each group separately. For each participant, real distractor source-level data (60-100 Hz, 0.1-0.3s) were baseline corrected by subtracting surrogate-distractor activity. For each group separately, corrected distractor gamma activity was contrasted between the two cue categories (informative vs. uninformative) using non-parametric cluster-based permutation testing. Only for the young group, a significant positive cluster ($p = 0.02$) was found in regions highly similar to that of the previous analysis: the dorso- and ventro-medial prefrontal cortices, the anterior cingulate gyrus, the pre- and post- central gyri, the supplementary motor area, the superior parietal lobule, in the left hemisphere (Figure 9B). All regions displayed a significantly higher gamma activation for trials when the distracting sound was preceded by an informative cue rather than an uninformative cue.

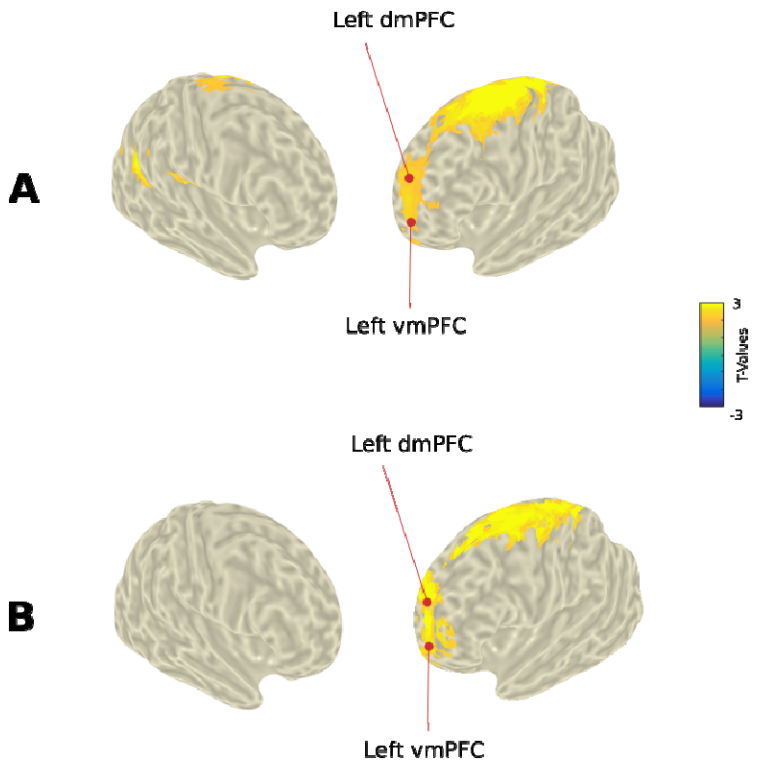

Figure 9. A. Between group comparison of gamma activity to distractor. Distributions of T-values, masked at *p<0.05*, from Cluster Based Permutation tests contrasting surrogate-corrected distractor gamma activity (60-100Hz and 0.1-0.3 post-distractor) between groups at the source level. Positive T-Values indicate stronger gamma activity in the young group. **B. Top-down modulation of gamma activity to distractor in the young group.** Distributions of T-values, masked at *p<0.05*, from Cluster Based Permutation tests contrasting surrogate-corrected distractor gamma activity (60-100Hz and 0.1-0.3 post-distractor) between informative and uninformative cue conditions for the young group. Positive T-Values indicate stronger gamma activity with informative cues. dmPFC: dorsomedial prefrontal cortex. vmPFC: ventro-medial prefrontal cortex.

4 Discussion

The present results demonstrate that ageing differently impacts TD and BU attentional processes. Behavioral measures of TD attention seemed unchanged while distractibility was exacerbated with ageing. Electrophysiologically, during anticipation of visually-cued sounds, the alpha power decrease in the relevant auditory cortices was preserved; whereas the alpha increase in the irrelevant visual areas was reduced, in elderly compared to young adults. Moreover, in response to distracting sounds, similar activation of the ventral BU attentional network, but reduced recruitment of medial frontal regions was observed in the gamma band, with ageing.

4.1 Impact of Ageing on Behavioral Measures of Attention

Behaviorally, both groups benefited from the cue information to faster discriminate the target pitch. This is in line with previous studies suggesting that TD attentional orienting is not affected by ageing (Greenwood et al., 1993; Curran et al., 2001; Olk and Kingstone, 2015; Erel and Levy, 2016).

In trials with distracting sounds, both groups displayed a similar reaction time (RT) pattern: participants were faster after early distracting sounds and slower after late distracting sounds, than with no distractors. This pattern could be explained in light of the effects triggered by distracting sounds (Bidet-Caulet et al., 2014; Masson and Bidet-Caulet, 2018): (1) a persistent increase in arousal resulting in a RT reduction and (2) a strong transient attentional capture (orienting) effect associated with a RT augmentation. The behavioral net effect of distracting sound varies according to the time interval between the distracting and the target sounds. Thus, with the present paradigm, the difference in RT to targets preceded by late distracting sounds (DIS2) and early distracting sounds (DIS1) provides a good approximation of the attentional capture effect with little contamination by arousal increases. Importantly, in comparison to the young group, elderly participants displayed a larger attentional capture effect. This increased susceptibility to task-irrelevant distractors is a recurrent finding in the literature using unimodal (visual or auditory) or cross-modal paradigms (e.g. Gazzaley et al., 2005; Parmentier and Andrés, 2009; Bélanger et al., 2010; Li and Zhao, 2015; Mevorach et al., 2016).

4.2 Impact of Ageing on TD Attentional Mechanisms

In the present study, we replicate with a slightly different protocol previous findings in young adults: during the anticipation of a visually-cued auditory target, (1) an increase in alpha power around 13 Hz in task-irrelevant visual regions is accompanied by (2) an alpha decrease around 9Hz in task-relevant auditory regions (ElShafei et al., 2018a). This suggests that alpha desynchronization and synchronization reflect facilitatory and suppressive mechanisms of TD attention, respectively, by augmenting and reducing cortical excitability (Klimesch et al., 2006; Jensen and Mazaheri, 2010; Foxe and Snyder 2011).

Noteworthy, we observed that elderly participants, compared to young adults, seem to display a similar alpha desynchronization in the relevant auditory cortices, but present a reduced alpha synchronization in the irrelevant visual cortices. These findings suggest that with ageing, suppressive TD attentional mechanisms become defect, while facilitatory mechanisms would be preserved, in line with (1) previous studies of alpha oscillations during visual attention (Vaden et al., 2012; Leenders et al., 2018), and (2) previous fMRI studies showing that filtering out task-irrelevant information is reduced with ageing (e.g. Gazzaley et al., 2005).

Moreover, we found a larger alpha desynchronization in the motor areas in the elderly, in agreement with an ageing-related stronger recruitment of motor regions during response preparation (e.g. Naccarato et al., 2006; Deiber et al., 2013). Elderly could rely more on motor preparation processes as a compensatory mechanism to their reduced attention filtering of irrelevant information, resulting in comparable performances to younger adults at the behavioral level.

Finally, a novel finding in the present study is the decreased differentiation between alpha peak frequency of different sensory regions, with ageing. This finding is in line with studies showing changes in alpha peak frequency across brain regions, through the life-span (e.g. Chiang et al., 2011; Gómez et al., 2013). Yet, this begs the question: is this decreased differentiation causal to the failure of older participants to filter out irrelevant visual information? Or does the alteration of suppressive attentional mechanisms result in a reduced alpha frequency specificity in the ageing brain? These questions remain for future investigation to answer.

4.3 Impact of Ageing on the TD/BU Attention balance

To the best of our knowledge, this is the first investigation of gamma activity to highlight the impact of ageing on auditory BU attentional processes. In both groups, gamma activation in bilateral auditory cortices, and several other brain regions including the temporo-parietal junctions and the right ventro-lateral prefrontal cortex, was observed in response to an unexpected salient distracting sound. These regions are part of the well-established ventral BU attentional network observed in fMRI (e.g. Salmi et al., 2009; Alho et al., 2014; Salo et al., 2017; Long and Kuhl, 2018) and electrophysiological (e.g. Ahveninen et al., 2013) studies. In the literature, it is rather unclear how ageing impacts the BU network with evidence of preserved (Deslauriers et al., 2017), reduced (Li et al., 2015) and even augmented (Kurth et al., 2016) activation with ageing. The present results suggest a similar activation of the ventral BU attentional network in the gamma band in elderly and young adults.

Importantly, younger participants demonstrated higher gamma activation than elderly ones in several regions outside the ventral network: mainly in the ventro- and dorso-medial prefrontal cortices (PFC) and the anterior cingulate cortex (ACC), in the left hemisphere. Interestingly, modulation of gamma activity according to the preceding cue information was found in the same brain regions only for young participants: gamma activity was larger after an informative cue in comparison to an uninformative cue. The ventro- and dorso-medial PFC and the ACC have been proposed to be part of the inhibitory control system. Their activation is increased during presentation of irrelevant salient stimuli (e.g. Salmi et al., 2009). In the non-human primate auditory system, cortico-cortical connections of these medial frontal regions to inhibitory neurons in auditory association regions support the suppression of irrelevant signals (Matsumoto and Tanaka, 2004; Barbas et al., 2005, 2012; Medalla et al., 2007). Direct evidence of an inhibitory role of these frontal regions has been found with electrical stimulation of the ACC resulting in reduced auditory evoked activity (Müller-Preuss et al., 1980; Müller-Preuss and Ploog, 1981). In human, medial PFC damage leads to enhanced EEG responses to distracting salient stimuli (Rule et al., 2002). We posit that, in the present study, gamma activation in the medial PFC regions and the ACC, during the presentation of distracting sounds reflects a strong and fast inhibitory signal to regions involved in the processing of task-irrelevant information. This inhibitory signal is enhanced with increased top-down attention load with informative cues, in young participants only. We found that with ageing the amplitude of this top-down inhibitory signal

decline in agreement with structural alterations in the PFC with ageing (e.g. Pardo et al., 2007). The capacity to modulate this inhibitory signal by TD attention is also altered in elderly, showing an imbalance in the BU/TD equilibrium with ageing. This is in line with a role of the medial frontal regions in the interaction between top-down and bottom-up networks of attention either directly (Salmi et al., 2009; Chadick et al., 2014) or indirectly via connections to the lateral prefrontal cortex (Medalla and Barbas, 2010).

4.4 Conclusion

To our knowledge, the current study is the first to utilize oscillatory modulations in the alpha and gamma bands to outline how ageing affects TD and BU attentional mechanisms and the interplay between them in the same experiment. Behaviorally, distractibility to salient unexpected sounds is exacerbated with ageing. Modulations in alpha oscillations reveal that while facilitatory processes of TD attention seem intact, suppressive processes are reduced with ageing, showing a less efficient TD filtering of task-irrelevant information. This deficit might be compensated by enhanced motor preparation. Moreover, modulations in gamma activity reveal that in comparison to younger adults, elderly participants similarly activate the ventral BU attentional network but display a weaker activation of inhibitory frontal regions in response to distracting sounds.

Therefore, the exacerbated distractibility exhibited by elderly participants at the behavioral level would rather be related to a reduced activation of TD inhibitory processes than to an enhanced activation of the ventral BU attentional network, leading to an attentional imbalance towards an enhanced impact of BU attention at the behavioral level. This potentially frontally-driven deterioration of TD attentional control in ageing lies on the cross-roads of the two leading hypotheses accounting for the increased distractibility often observed with ageing: the inhibitory deficit (Hasher and Zacks, 1988) and the frontal ageing (West, 1996) hypotheses. In line with previous findings (Chadick et al., 2014; Amer et al., 2016) and with the proposition made by Gazzaley and D'Esposito (2007), our findings reconcile both hypotheses: the decrease in the functioning of the frontal control network might be the origin of the ageing-related deficit in inhibitory mechanisms.

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