Brain oscillations in cognitive control: a cross-sectional study with a spatial Stroop task

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Abstract

An important aspect of cognitive control is the ability to overcome interference, by boosting the processing of task-relevant information while suppressing the irrelevant information. This ability is affected by the progressive cognitive decline observed in aging. The aims of this study were to shed light on the neural spectral dynamics involved in interference control and to investigate age-dependent differences in these dynamics. For these reasons two samples of participants of different ages (23 younger and 20 older adults, age range = [18 35] and [66 82], respectively) were recruited and administered a spatial Stroop task while recording electroencephalographic activity. Scalp- and source-based time-frequency analyses revealed a main role of theta and beta frequencies in interference control. Specifically, for the theta band, we found age-dependent differences both for early event-related spectral perturbation (ERSP) Stroop effects at the source level – which involved dorsomedial and dorsolateral prefrontal cortices – and for related brain-behaviour correlations. This ERSP Stroop effect in theta was greatly reduced in magnitude in the older group and, differently from what observed in younger participants, it was not correlated with behavioural performance. These results suggest an age-dependent impairment of the theta-related mechanism signalling the need of cognitive control, in line with existing findings. We also found age-related differences in ERSP and source spectral activity involving beta frequencies. Indeed, younger participants showed a specific ERSP Stroop effect in beta – with the main involvement of left prefrontal cortex – whereas the pattern of older participants was delayed in time and spread bilaterally over the scalp. This study shows clear age-related differences in the neural spectral correlates of cognitive control. These findings open new questions about the causal involvement of specific oscillations in different cognitive processes and may inspire future interventions against age-related cognitive decline.

Keywords: time-frequency analysis, interference control, EEG, cognitive aging, distributed source reconstruction, Stroop effect.

Highlights

- We studied spectral correlates of interference control in younger and older participants.
- We found clear scalp and source-based group differences in midfrontal theta and prefrontal beta bands.
- Theta band marking the need of cognitive control was reduced in older adults.
- Beta activity was increased in older adults, in line with age-related dedifferentiation theories.

Introduction

The ability to select relevant information and to ignore the conflicting and irrelevant information is a core aspect of cognitive control, and it allows us to flexibly adapt our behaviour (Miller and Cohen, 2001). Understanding the neural underpinnings of this cognitive function remains challenging. Many experimental designs have been adopted to investigate the selection of task relevant features and the Stroop paradigm is one of the most widely used to study how we resist to the interference of irrelevant information (Macleod, 1991; Stroop, 1935). Previous studies suggested that the cognitive processes involved in this task engages the left lateral portion of the prefrontal cortex (PFC), independently of the stimulus domain, as for example the verbal or spatial domain (see Vallesi, 2012, for a review). A model of executive functions, which is based on the case of interference control in the Stroop task, suggested that this function can be considered as a temporal cascade of processes selection (Banich, 2009). This Cascade of Control Model suggests that the dorsolateral PFC (DLPFC) creates and imposes a top-down attentional set for task-relevant goals, thus applying a bias to specific task-relevant processes and representations, especially those needed when other competing but irrelevant processes must be suppressed. After setting the attentional bias, posterior regions of dorsal anterior cingulate cortex (dACC) are hypothesized to be involved in processes of responses selection, whereas the more anterior portions are engaged in the evaluation of the output. Notably, as highlighted by the author, the more efficient the control exerted by DLPFC regions is, the less the recruitment of dACC regions is. This is corroborated by evidence showing that older adults, who recruited less the DLPFC, showed increased activation of ACC, meaning that there is probably a failure in the effectiveness of DLPFC control (Milham et al., 2002). A similar pattern of anti-correlation between the activation of these two regions has also been observed in younger adults (e.g., Floden et al., 2011).

Indeed, how executive functions change across the lifespan is another important issue to solve. As social and health conditions improve, also life expectancy increases, and the number of people over 65 years old is rapidly rising (He et al., 2016). It is well established that healthy aging entails a progressive cognitive decline, the causes of which are still unknown. It has been proposed that a general slowing of processing speed can be responsible for the performance decrease in older adults documented in different tasks (Verhaeghen and De Meersman, 1998). However, other evidence suggested that this slowing cannot be the only answer and that there must be other changes contributing to it (Bugg et al., 2007; Forstmann et al., 2011). Indeed, neuroimaging studies reported age-related changes in the brain both anatomically (see Fjell and Walhovd, 2010, for a review) and functionally (Greenwood, 2000), spanning a variety of functions, such as working memory, attention, interference control, inhibition of irrelevant information (Gazzaley and D'esposito, 2007; Hasher and Zacks, 1988; Vallesi et al., 2009; West, 2004). Moreover, age-related changes in cerebral anatomy and physiology have been proposed to lead to a general reorganization of brain functions, especially concerning the prefrontal cortex. In particular, it has been reported that older adults show less lateralized activity over prefrontal regions during cognitive tasks (e.g., hemispheric asymmetry reduction in older adults –HAROLD– model, see Cabeza, 2002). Moreover, other evidence indicates an age-related increase in frontal activity, suggested to be an indicator of compensatory mechanisms carried out to face the structural and functional age-related decline (e.g., scaffolding theory of aging and cognition, see Park and Reuter-Lorenz, 2009; Reuter-Lorenz and Park, 2014). It is important to shed light on which mechanisms are mainly subjected to these modifications and how they differ from normal functioning, in order to find potential therapies, treatments, or training that can reduce this deterioration.

The aforementioned issues constituted the starting points for the present electroencephalographic (EEG) study, in which we had multiple aims. In particular, we investigated event-related spectral perturbation (ERSP) of interference control and if these spectral dynamics change during adult lifespan. For these reasons, we recruited two samples of participants of different ages and conducted time-frequency analysis, which has the advantage (when compared to the event-related potential method) to providing information about the time course of the involvement of different frequency bands in specific cognitive tasks (Engel and Fries, 2010). Indeed, this analysis allows extracting information about power changes in each frequency under examination and their changes during time with regard to task events (extracting the so-called event-related spectral perturbation), so that different neural oscillation can be linked to many different cognitive processes (Roach and Mathalon, 2008). This approach has been gaining attention over the last years and different studies suggested that oscillatory activity plays a key role in neural communication and other cognitive functions (Fries, 2005; Salinas and Sejnowski, 2001).

Moreover, we aimed at reconstructing the cortical sources of spectral dynamics to shed light on the contribution of left and right DLPFC in the process of interference control, as previous studies suggested the domain-general activation of the left portion (see Vallesi, 2012, for a review). Hence, we employed a spatial version of the Stroop task, since processing of non-verbal information is thought to be lateralized over the right hemisphere (Boulinguez et al., 2003; Weintraub and Mesulam, 1987). Thus, finding left lateralized spectral correlates for interference control using spatial material would allow drawing more compelling conclusions about the domain-independent asymmetry of executive functions.

Concerning the implications of spectral dynamics in cognitive tasks, a general integrative role has been attributed to theta band activity (4-7 Hz) in the organization of brain activity (Sauseng et al., 2010). More specifically, mid-frontal oscillations in the theta band have been identified as the mostly implied frequency in interference control and conflict processing, reflecting the need for cognitive control (Cavanagh and Frank, 2014; Cohen, 2014). Previous studies using colour-word

Stroop tasks with manual responses reported an increase in mid-frontal theta power for incongruent conditions (Ergen et al., 2014; Hanslmayr et al., 2008; see also Wang et al., 2014; Zhao et al., 2015). Evidence from other spatial paradigms, such as the Flanker task, also showed increase in mid-frontal theta power for higher cognitive demands when responding to incongruent trials (Nigbur et al., 2011; see also Zavala et al., 2013). On the basis of these results, we expect to find evidence for an early temporal involvement of theta band, with a mid-frontal increase in theta power for incongruent condition, reflecting a general signal for the need to exert cognitive control.

Other studies have evidenced the role of beta oscillations (13-30 Hz) in interference control. In particular, in a previous study from our laboratory (Ambrosini and Vallesi, 2017), we found that the prefrontal hemispheric asymmetry in beta electrophysiological activity at rest correlated with the participants' ability to control interference in verbal and spatial versions of the Stroop task. Moreover, studies aimed at disentangling conflict associated with stimuli and responses by administering modified versions of the Stroop tasks (i.e., combination of Simon and Stroop task or 2-1 mapping task) showed the involvement of beta band power modulations in response conflict (Wang et al., 2014; Zhao et al., 2015), with a conflict-induced reduction of beta spectral power. Results from another study using intracranial recording revealed greater desynchronization in beta and alpha activity in medial prefrontal cortex for the incongruent condition (Aulická et al., 2014). We thus also expect to find evidence for the involvement of beta frequencies in Stroop performance. Specifically, given the role of theta modulations in signalling the need for cognitive control, we expect beta band modulations to be implicated in later time windows in order to cope with the Stroop interference. In particular, we hypothesize that the cognitive processes implicated in the resolution of Stroop interference, such as the selection of task-relevant representations or appropriate responses, may be translated in the recruitment of beta band, possibly with a left lateralization of prefrontal involvement.

As regards age-related differences in ERSP correlates of cognitive control, we expect to find a general over-recruitment of neural resources in older adults, in line with the scaffolding theory (Park and Reuter-Lorenz, 2009). Moreover, in line with the HAROLD model, we expect to find an age-dependent reduction of the left-lateralized prefrontal asymmetry that has been related to interference control and Stroop performance in young participants (see Ambrosini and Vallesi, 2017; see also Vallesi, 2012, for a review).

Methods

Participants

The initial sample was composed of 24 younger adults (females = 13, mean age = 25.58 years, SD = 4.73 years, range = [18 35] years) and 21 older adults (females = 10, mean age = 72.86 years, SD = 4.55 years, age range = [66 82] years). One younger and one older participant were excluded because they did not complete the task. The final sample was thus composed of 23 younger adults (females = 12, mean age = 25.26 years, SD = 4.55 years, range = [18 35] years) and 20 older adults (females = 9, mean age = 73.2 years, SD = 4.38 years, age range = [66 82] years). There were no gender differences between the two groups ($p > .7626$, two-tailed Fisher's exact test). Behavioural data from one female participant from the younger group were not recorded due to technical problems, so she was removed from behavioural and correlation analyses; one male participant from the same group was excluded from electrophysiological and correlation analyses due to technical problems in EEG recording that compromised EEG data quality. All participants met the inclusion criteria to take part to this study, which were being native Italian speakers, right-handed, having normal or corrected-to-normal visual acuity, having no current or major past neurological or psychiatric disorders, and having no cognitive decline or dementia for the older adults. The Edinburgh Handedness Inventory (Oldfield, 1971) was used to measure participants' handedness. Participants were selected in order to match the two age-groups for years of formal education (younger: *M* = 13.3 years, *SD* = 4.24 years; older: *M* = 14.25 years, *SD* = 4.28 years; $t_{(40)}$ = .472, *p* = .726). Older adults were screened for dementia using the Montreal Cognitive Assessment (MoCA) (Nasreddine et al., 2005) (*M* = 27, *SD* = .92, range: [26 29]) and only participants with a score ≥ 26 were included. All the participants signed an informed consent before taking part to the study and were reimbursed € 25 for their time. The study was approved by the SISSA Ethical Committee in Trieste.

Design and stimuli

We used a 4-choice version of the spatial Stroop task previously used by Puccioni and Vallesi (2012)[1], a cognitive conflict task including both stimulus-stimulus and stimulus-response interference. This task was implemented as a priming-free task (by avoiding partial and total feature repetitions in first-order trial sequences), in order to explore age-related differences in interference control, avoiding possible additional confounds. The stimuli were arrows pointing toward one of the four corners of the screen and appearing in one of the same four screen portions (upper-left, upper-right, lower-left, lower-right). Specifically, the stimuli were presented less than 5 cm above/below and on the left/right from the center of the screen and participants were asked to try maintaining their gaze at the center of the screen during task execution. Participants were instructed to ignore the location where the stimulus appeared and to pay attention to the direction towards which the arrow pointed, by pressing the corresponding button on a response pad using index and middle fingers of both hands (the buttons were spatially arranged in a configuration that corresponded to the spatial location of the stimuli). The instructions were as follows: "You are going to see some

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[1] This experimental task entails some features in common with tasks used to investigate the Simon effect, in that the spatial position of the response and that of the stimulus (i.e., the task-irrelevant feature) may or may not correspond. However, differently from the Simon task, in our experimental task the task-relevant feature of the stimuli was spatial in nature (i.e., the arrow direction). Moreover, Stroop and Simon tasks can be differentiated by assessing the effect of the task-irrelevant information on response time distribution by means of delta plots (see Pratte et al., 2010). We conducted this analysis and we found that the distribution resembles the one commonly seen for Stroop tasks, which has an opposite pattern compared to the one typical for Simon tasks.

arrows, which will appear one at a time in one of the four corners of the screen. We ask you to press the button of the response pad corresponding to the direction indicated by the arrow. You will need to use the index and middle fingers of both hands. Please, try to respond as fast and accurate as possible". The stimuli were defined as congruent when location and direction of the arrow matched (e.g., an arrow pointing toward upper-right corner and appearing in the upper-right portion of the screen), and as incongruent when they differed (e.g., an arrow pointing toward upper-right corner but appearing in the lower-left portion of the screen). The stimuli were equally divided in congruent and incongruent conditions and appeared in a pseudorandom order, so that there were no repetitions of the same location or direction on subsequent trials, to minimize any type of priming. The task consisted of a training phase of 16 trials performed until participants reached 10 correct answers, and a test phase separated in three different blocks each one composed of 2 sub-blocks of 64 stimuli each. The stimuli were presented over a light grey background with a fixation cross at the center of the screen. The target lasted for 500 ms, followed by a blank screen for 2000 ms when it was possible to give the response. Subsequently, it was presented an extra blank screen randomly lasting between 250 and 700 ms that constituted the inter-trial-interval (see Figure 1).

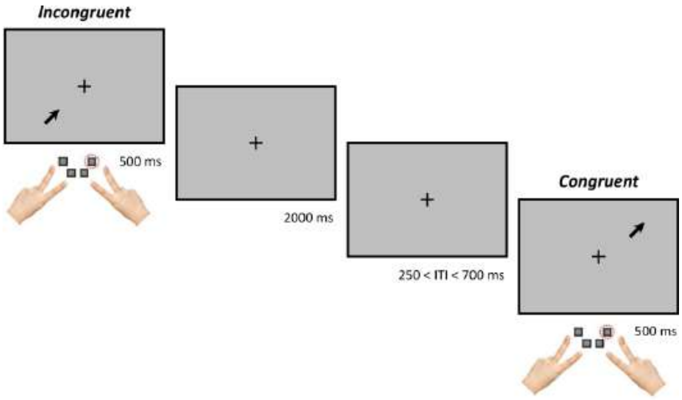

Figure 1. Experimental paradigm.

The figure shows an example of the experimental design. Each of the experimental stimuli appeared for 500 ms, followed by a blank screen lasting 2000 ms. The inter-trial-interval appeared as an extra blank screen randomly lasting between 250 and 700 ms. The figure shows an example of incongruent and congruent trials. Participants were asked to respond by pressing the response button corresponding to the direction indicated by the arrow, while ignoring its spatial position (in the example above, correct responses are highlighted by a red dashed circle).

EEG recording

All data were recorded using a Biosemi^{TM} ActiveTwo 128-channel system with sintered Ag/AgCl electrodes. The recording was sampled at 256 Hz and referenced online to the mastoid electrodes. Electrooculographic (EOG) activity was recorded by means of four electrodes placed on right and left external canthi and infra-orbital ridges of each participant. Four additional electrodes were placed on mastoids and peri-auricular areas to record muscular activity. All electrodes were adjusted to maintain their offset below 40 mV and impedance below 10 KΩ.

Data analysis

Behavioural analysis

Data from error trials and post-error trials (respectively, 3.94% and 3.63% of the experimental trials) were not included in the analysis of response times (RTs). RTs were log-transformed to improve normality and mitigate the near-multiplicative effects of the general slowing in RT observed in previous aging studies (Cerella, 1990; Faust et al., 1999). Moreover, those log-RTs above and below two standard deviations (*SD*) from the mean calculated for each participant and condition were excluded (6.47% of the valid trials). Percentage of accuracy and mean RTs were analysed using a 2x2 mixed-design ANOVA with trial Congruency (within-subjects) and Age Group (between subjects) as factors.

Electrophysiological analysis

Offline signal pre-processing was performed using MATLAB (Version R2013b; The MathWorks, Inc., Natick, MA) scripts created ad-hoc based on the functions from the EEGLAB toolbox (version 13.4.4b; Delorme and Makeig, 2004). Raw continuous recordings were filtered offline using a zero-phase

Hamming windowed sinc FIR filter (cut-off frequencies: 0.05 and 45 Hz, transition bandwidth: 0.1 and 10 Hz, passband edges: 0.1 and 40 Hz) and subsequently bad channels were detected and removed by means of the *clean_rawdata* EEGLAB plugin using the Artifact Subspace Reconstruction (ASR; the autocorrelation parameter was set at 0.8, leading to the exclusion of 3.5 channels on average, *SD* = 4, see Mullen et al., 2013). There was no significant difference in the number of removed channels between younger ($M = 3.73$, $SD = 7.71$) and older participants ($M = 4.25$, $SD = 3.19$): $t_{(40)} = -0.28$, $p = .78$. Data were then segmented into epochs (from -1200 ms to 2700 ms) with respect to the stimulus onset and erroneous trials were excluded from further analyses[2]. Independent component analysis was then applied to correct for eye movements and blinks based on scalp topography, evoked time courses and spectral distribution. Visual inspection of the resulting ERP traces confirmed the absence of residual artifacts related to eye movements and blinks. Baseline correction from -200 to 0 ms was then used, followed by spherical spline interpolation of bad channels (Perrin et al., 1989). Data were then re-referenced to a common average reference. Detection of artifactual epochs was performed by means of an automatic procedure based on extreme values thresholding (+/- 200 µV) and improbability and kurtosis criteria (SD > 7 for single channel and SD > 3 for global threshold); epochs that violated one or more of these criteria were excluded from further analyses (Delorme et al., 2007). The minimum number of epochs used for the analysis was 136 (younger: *M* = 181 and 172, range = [165 187] and [153 186] for congruent and incongruent trials, respectively; older: *M* = 176 and 172, range = [170 184] and [136 188] for congruent and incongruent trials, respectively). There was no significant difference between groups and congruency in the number of epochs used for further analysis ($F_{(1,40)} = 1.84$, $p > .18$).

We extracted event related spectral perturbation (ERSP) in the frequency range between 4 and 45 Hz (linearly spaced, 1 Hz resolution) using wavelets with a temporal window of approximately

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[2] We did not exclude post-error trials from the EEG analysis because of a mistake in the analysis pipeline. Nonetheless, the proportion of post-error trials was very small ($M = 3.9\%$, $SD = 3.07\%$) and it was not significantly different between conditions or groups. More importantly, the general pattern of ERSP results was confirmed when excluding post-error trials from analyses.

560 ms and corresponding to a linearly increasing number of cycles (from 2 to 22.5 cycles for the 4 and 45 Hz frequencies, respectively); the baseline correction was applied trial by trial using the average power in the time window from 800 to 300 ms before stimulus onset.

Differences in ERSP due to the Stroop effect were tested for statistical significance through the threshold-free cluster-enhancement (TFCE) method, which optimizes the detection of diffuse, low amplitude signal while correcting for multiple comparisons ($p < 0.05$) (Smith and Nichols, 2009). This method was applied on the entire channel-time-frequency space by taking into account all the 128 channels, 200 timepoints covering a time window ranging approximately from -650 ms to 2150 ms (and thus excluding edge artifacts resulting from the wavelet transform and precluding across-trials overlapping of the stimulus-related activity of interest) with a resolution of about 15 ms, and all the 42 frequencies ranging from 4 to 45 Hz. However, in order to facilitate the description of the results, we will refer to the following frequency bands: theta (4-7 Hz), alpha (8-12 Hz), beta1 (13-18 Hz), beta2 (19-24 Hz), beta3 (25-30 Hz), lower gamma (31-45 Hz). This analysis of ERSP at the scalp level was performed to allow for better comparison with previous (e.g., Wang et al., 2017; Zaho et al., 2014) and future studies.

We first assessed the significance of the ERSP Stroop effect in younger and older participants, thus testing for the simple effects of the Congruency factor (incongruent vs. congruent Stroop condition) in each age group. We then assessed whether age significantly modulated the ERSP Stroop effect by contrasting it between younger and older participants. This analysis thus tested for the interaction between Congruency and Group (older vs younger), that is, the effect of primary theoretical interest. Note that we report the results of the simple effects of the Congruency factor for each age group separately in order to facilitate the interpretation of the interaction between Congruency and Group (older vs younger).

All the results reported in the test were significant at an alpha level of .05 both at the single spatio-temporo-spectral sample level and at the cluster level, thus corresponding to a critical *t* value of ±2.02 (df = 40).

Distributed source estimation

As detailed in the Introduction, we aimed to shed light on the contribution of prefrontal functional hemispheric asymmetries in mediating interference control processes. To this aim, we estimated the neuronal source of our main scalp-based time-frequency effects using Brainstorm toolbox (Tadel et al., 2011). In particular, we estimated the current strength dynamics of the EEG cortical sources using the depth-weighted minimum norm estimation approach (Baillet et al., 2001) and a boundary element methods (BEM) conductive head model (Gramfort et al., 2010; Kybic et al., 2005). The solution space was constrained to the cerebral cortex, which was modeled as a three-dimensional grid of 15002 elementary current dipoles based on the FreeSurfer brain template (FSAverage; see Fischl et al., 1999). The results were then tested for statistical significance by using again the TFCE method by taking into account all the 15002 vertices, all the 200 original time points, and all the 42 frequencies ranging from 4 to 45 Hz. Therefore, there was no selection of the spatio-temporo-spectral data based on the results of the scalp-level analyses, thus avoiding the circularity problem.

Time-frequency – behaviour correlation analysis

We used Pearson's correlation to test for associations between behavioural and electrophysiological measures. In particular, for each age group, we first computed the correlations between the participants' RT Stroop effect (i.e., the incongruent – congruent difference in RTs) and the corresponding ERSP Stroop effect (i.e., the incongruent – congruent difference in the ERSP) in all frequencies, time points, and channels, and assessed their statistical significance using the TFCE method. We then compared the Fisher-transformed correlations in older and younger participants by means of the Fisher's *Z* test and corrected the results for multiple comparisons using the TFCE method. The Fisher's *Z* test is specifically designed to test for statistically significant differences in correlations between two independent groups, thus allowing us to test for age-dependent modulations of the brain-behaviour correlations.

We chose to perform the TFCE mass univariate analyses for the ERSP Stroop effects extracted at the scalp level, instead of those extracted at the source level, again because the latter is extremely computationally intensive and time-consuming. In this way, we also hoped to facilitate the comparison between our results and previous and future literature.

Results

Subject-level behavioural and EEG time-frequency data supporting the conclusions are made available at Open Science Framework (https://osf.io/3wmg4) under a CC-BY 4.0 license, in compliance with the requirements of the funding body (ERC) and the institutional ethics approval.

Behavioural results

Table 1 shows descriptive statistics for the behavioural results. On average, all participants reported faster RTs for congruent trials compared to incongruent trials, as demonstrated by a significant main effect of Congruency ($F_{(1,40)} = 307.49$, $p < .0001$, $\eta^2_p = .88$). There was also a main effect of Group ($F_{(1,40)} = 67.37$, $p < .0001$, $\eta^2_p = .63$) due to older participants showing longer RTs than younger controls. The interaction between Congruency and Group was also significant ($F_{(1,40)} = 4.19$, $p = .047$, $\eta^2_p = .09$), meaning that the Stroop effect was higher in the older group as compared to the younger one.

Concerning accuracy, the ANOVA revealed a significant main effect of trial Congruency only, so that a higher percentage of correct responses was given for congruent trials ($F_{(1,40)} = 46.23$, $p < .0001$, $\eta^2_p = .54$). Accuracy did not significantly differ between groups ($F_{(1,40)} = 0.21$, $p = .65$, $\eta^2_p < .01$)

and the interaction was not significant ($F_{(1,40)} = 0.04$, $p = .83$, $\eta^2_p < .01$) (see Figure 2). Note that the results did not change when performing non-parametric analyses.

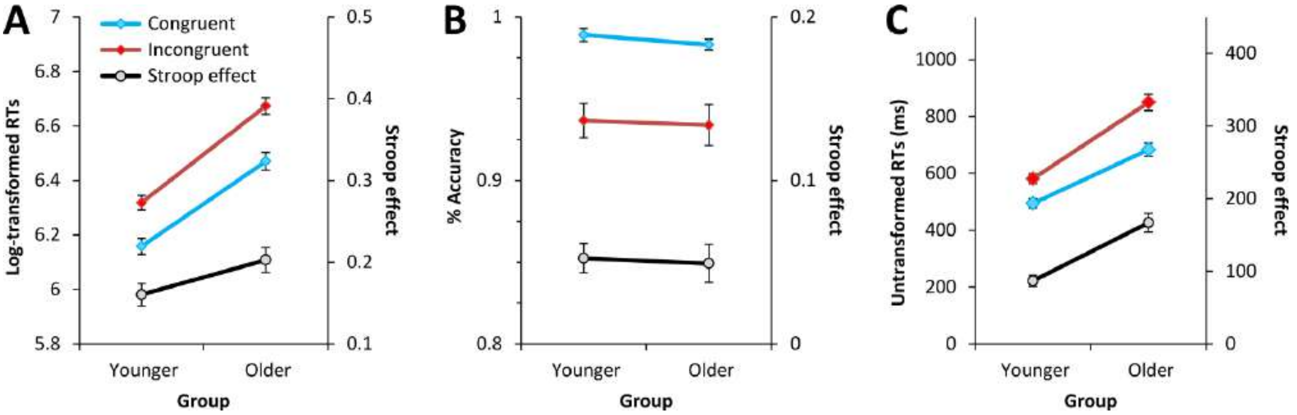

Figure 2. Behavioural results.
The figure shows results for log-transformed RTs (A), accuracy (B), and untransformed RTs (C) as a function of the age Group (x axis) and Congruency factors. The dark red line corresponds to the incongruent trials, and the light blue one to the congruent ones (left y axis). Black lines represent the Stroop effect (i.e., the Incongruent – Congruent difference; right y axis). Error bars indicate standard errors of the mean.

Table 1. Descriptive statistics for behavioural results.

	Congruent		Incongruent		Stroop effect	
	M	*SD*	*M*	*SD*	*M*	*SD*
Log-transformed RTs						
Younger	6.158	0.136	6.318	0.126	0.160	0.064
Older	6.470	0.144	6.673	0.138	0.203	0.071
Untransformed RTs (ms)						
Younger	494	78	581	81	87	38
Older	683	106	850	131	167	60
Accuracy (%)						
Younger	98.9	1.8	93.7	4.9	5.2	4.2
Older	98.3	1.5	93.4	5.6	4.9	5.5

Scalp-based time-frequency

The analysis on younger participants revealed a number of significant ERSP Stroop effects mainly involving beta frequencies over parieto-occipital and frontal channels and gamma frequencies over centro-parietal channels in relatively early time windows (see Figure 3). Specifically, a first cluster showing significant ERSP Stroop effects in the beta2 range was observed over frontal channels, with a slight left lateralization, in a time window approximately ranging from 350 to 950 ms (see Figures 3 and 4a, b). A second cluster involving beta2 frequencies was observed over centro-parietal and parieto-occipital channels, again with a slight left lateralization. However, this posterior effect was temporally and spectrally less specific. Indeed, in this case the ERSP Stroop effect in the beta2 band was earlier and more sustained and it also involved surrounding beta1, beta3, and gamma frequency bands, as well as alpha frequencies over centro-parietal channels in a later time window starting approximately at 1000 ms (see Figure 3). All these effects were due to a stronger event-related decrease in power for incongruent condition as compared to the congruent one. We also observed a third independent, small cluster involving theta frequencies over left parietal channels in an early time window approximately ranging from 250 to 450 ms. This effect was due to a stronger event-related increase in theta power for congruent as compared to incongruent condition.

The analysis on older participants revealed a pattern of significant ERSP Stroop effects that also involved mainly beta and gamma frequencies, but that was less specific both spatially and temporally. Specifically, a first large cluster showing significant ERSP Stroop effects in the beta and gamma frequencies was observed over most of the scalp, with the exclusion of lateral frontal and fronto-temporal channels, in a time window that mainly ranged from 600 to 1400 ms but also included later samples (see Figures 3 and 4c, d). As for younger participants, these effects were due to a stronger event-related decrease in power for the incongruent condition with respect to the congruent one. We also observed a second, partially independent, small cluster involving theta frequencies over bilateral posterior channels in an early time window approximately ranging from 0 to 1200 ms, which also involved alpha frequencies in a later time window (from 750 to 1200 ms) (see Figures 3 and 4c, d). This effect was due to a stronger event-related increase in theta power for the congruent condition as compared to the incongruent one.

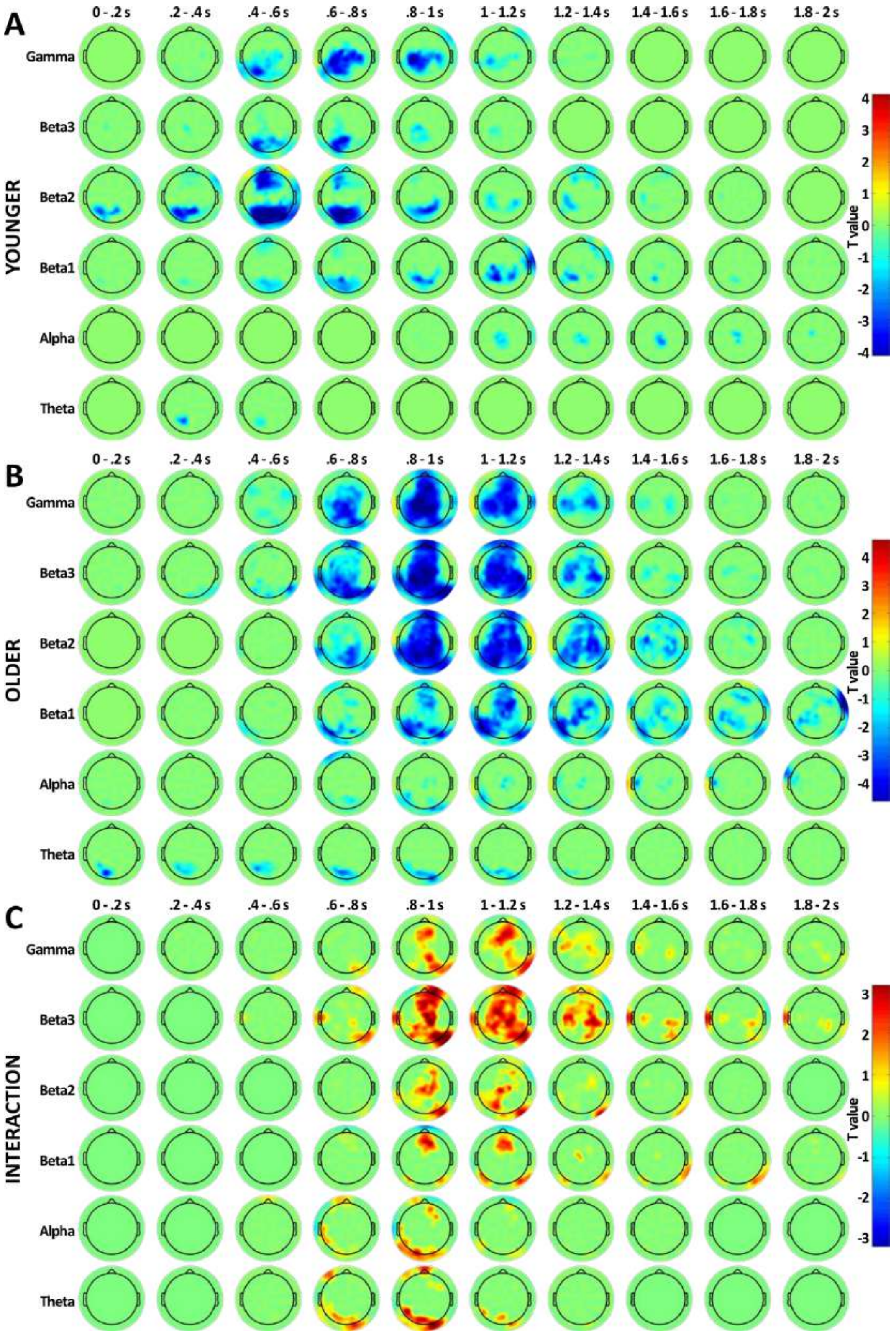

Figure 3 – Results of the scalp-based event-related spectral perturbation (ERSP) analysis.
The figure shows the topoplots for the results of simple effect analysis in younger (A) and older (B) participants, as well as the results of the interaction analysis (C). Each row represents the average of each frequency band, whereas the columns represents the average of EEG activity every 200 ms after stimulus presentation (time 0). The topoplots show the *t values* of the significant results after TFCE. Younger participants' results evidenced a major involvement of higher frequencies range and in particular of beta2. In this band, the activity arose after stimulus presentation from posterior regions and it moved anteriorly showing a left lateralization during the time period preceding the response (400-600 ms). For older participants, higher frequencies bands, from beta1 to gamma, were mostly involved. The activity occurred around the response time (600-800 ms) and involved channels spread all over the scalp. These differences were reflected in the topoplots for the interaction analysis.

These analyses indicate the existence of age-dependent modulations of ERSP Stroop effects, as older participants showed later and more widespread and unspecific spectral correlates of interference control processes. This pattern was confirmed by the analysis contrasting the ERSP Stroop effects between younger and older participants, which showed a number of significant age-dependent modulations of ERSP Stroop effects mainly involving higher frequencies (>12 Hz) over parietal and frontal channels and lower frequencies (<12 Hz) over parieto-occipital channels in a time windows ranging from 600 to 1200 ms (see Figure 3). Overall, this pattern of results closely resembles that observed for the simple effect analysis on older participants. Specifically, a first large cluster showing significant ERSP Stroop effects in the beta and gamma frequencies was observed across a number of electrodes spread over the scalp in a time window that mainly ranged from 600 to 1400 ms but also included later samples (see Figures 3 and 4a, b). These effects were characterized by stronger ERSP Stroop effects in older as compared to younger participants. Specifically, this pattern of results was due to the fact that in older participants, as compared to younger ones, the stronger event-related decrease in power for the incongruent condition was more pronounced over central electrodes and, generally, involved a higher number of frequencies over a higher number of channels in a later and more sustained time window (see Figure 3). In particular, while the event-related decrease in beta power occurred at around the same time for both age groups and congruency conditions, the decrease in beta power for incongruent as compared to congruent condition was more sustained for older participants. Consequently, the ERSP Stroop effect occurred later ad was more sustained in this age group.

We also observed a second cluster involving theta and alpha frequencies over bilateral posterior channels in an earlier time window approximately ranging from 600 to 1200 ms (see Figures 3 and 4c, d). This effect was due to the fact that in older participants, as compared to younger ones, there was a stronger event-related increase in low-frequency power for the congruent condition as compared to the incongruent one.

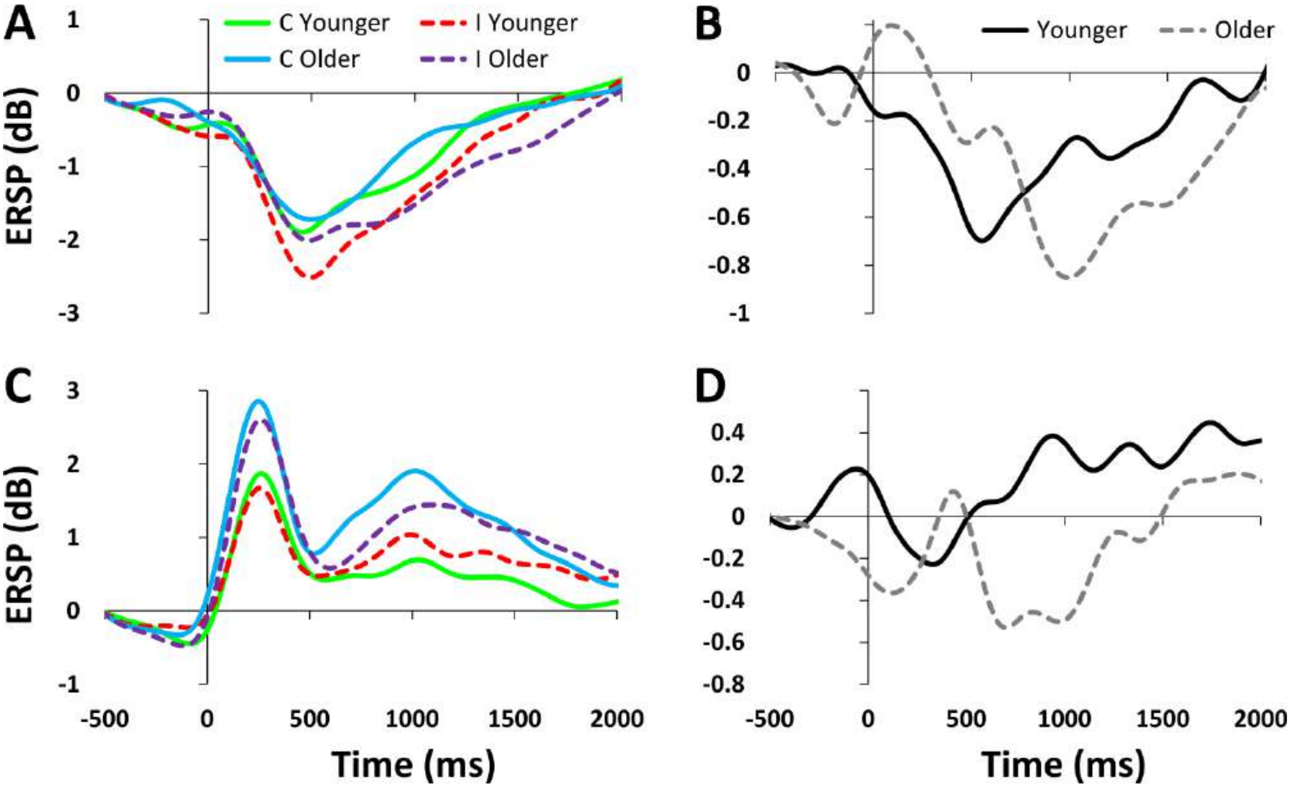

Figure 4 – Representative results from the scalp-based ERSP analysis.
The plots show the ERSP traces for the results of simple effect analysis in younger and older participants for the beta (A) and theta (C) bands, as well as the results of the interaction analysis for the same frequencies (respectively, B and D). The plots in (A) and (B) depicts representative data for a frequency in the beta2 band (20 Hz) extracted from a channel in the mid-frontal cluster (Fz), while the plots in (C) and (D) depicts representative data for a frequency in the theta band (7 Hz) extracted from a channel in the posterior cluster (POz) (see text for details).

To sum up, results from the interaction between Congruency and Group revealed significant effects in all the frequency bands taken into account for this study, which were driven by the ERSP Stroop effects observed in the group of older participants. Overall, higher frequencies, from beta to gamma, seem to be especially involved in interference control processes, as summarized in Figure 3. Importantly, younger participants mainly engaged frequencies in the beta2 range, with Stroop-dependent modulations starting soon after stimulus presentation on posterior regions and gradually moving over left frontal electrodes, until the time window close to the response. Older participants mainly recruited all the frequencies higher than 12 Hz (from beta1 to gamma bands), and this activity started around the time window of the response engaging electrodes spread over the scalp. For these frequencies and for both groups, incongruent trials yielded a stronger power suppression as compared to the congruent ones.

Regarding the theta band, the scalp-based ERSP analysis showed an unexpected pattern of age-dependent results: a greater increase of power was observed for the congruent condition over posterior channels, while no age-dependent power increase was observed for the incongruent condition over mid-frontal channels, contrary to what we hypothesized (see Introduction).

Source-based time-frequency analyses

We computed ERSP data based on the reconstructed cortical sources of electrophysiological activity and performed the same TFCE analysis as for scalp-based ERSP data. The analysis revealed a very high number of significant age-dependent modulations of the ERSP Stroop effects. However, for the sake of conciseness and readability, we report here only the results for the two spectral bands for which we had strong a-priori hypotheses about their cortical localization, as detailed in the Introduction: 1) the theta band, for which a large body of evidence suggests the involvement of the medial prefrontal cortex in signalling the need for cognitive control, and 2) the beta2 band, for which we expected to find evidence for the involvement of the DLPFC in mediating interference control processes, with a particular interest in assessing possible hemispheric asymmetries.

As regards the theta band, the Group by Congruency interaction was significant in a time window from around 200 ms to 600 ms over bilateral and medial dorsal frontal regions, where cortical sources showed a stronger incongruency-dependent power increase for younger as compared to older participants. This result was mainly due to an earlier and stronger ERSP Stroop effect in younger participants as compared to older ones. Indeed, simple effect analysis showed that younger participants exhibited a significant incongruency-dependent power increase starting from

200 ms mainly involving bilateral dorsolateral and dorsomedial prefrontal regions. By contrast, the same power modulation was almost absent in older participants (Figure 5)[3].

The results for the beta2 band generally confirmed the impressions derived from the corresponding scalp-based analysis. Indeed, the Group by Congruency interaction was significant in a temporal window from around 600 ms to 2000 ms over bilateral dorsal frontal and parietal regions, where cortical sources showed a stronger incongruency-dependent power decrease for the older group as compared to the younger one. Again, this result was mainly due to a later and more widespread ERSP Stroop effect in older participants as compared to younger ones. Indeed, simple effect analysis showed that younger participants exhibited a significant incongruency-dependent power decrease starting from approximately 300 ms with a clear left prefrontal lateralization involving the middle and superior frontal gyri. By contrast, older participants did not show significant incongruency-dependent power modulations until around 600 ms, which originated in bilateral medial parietal regions and then rapidly spread over extended portions of bilateral dorsal frontal and parietal cortices, lasting even after the power modulation in younger participants disappeared (Figure 5).

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[3] We think that this result is not related to the theta-related effect that we observed in the scalp-based analysis over posterior channels. Indeed, the cortical distribution of the sources showing the significant theta-related effects is hardly consistent with the scalp distribution of the channels showing the significant theta-related effects. Moreover, the scalp-based and the source-based theta effects also have opposite pattern of power increase as regards the experimental conditions, as a greater increase of power was observed for the congruent and incongruent conditions, respectively, in the two analyses.

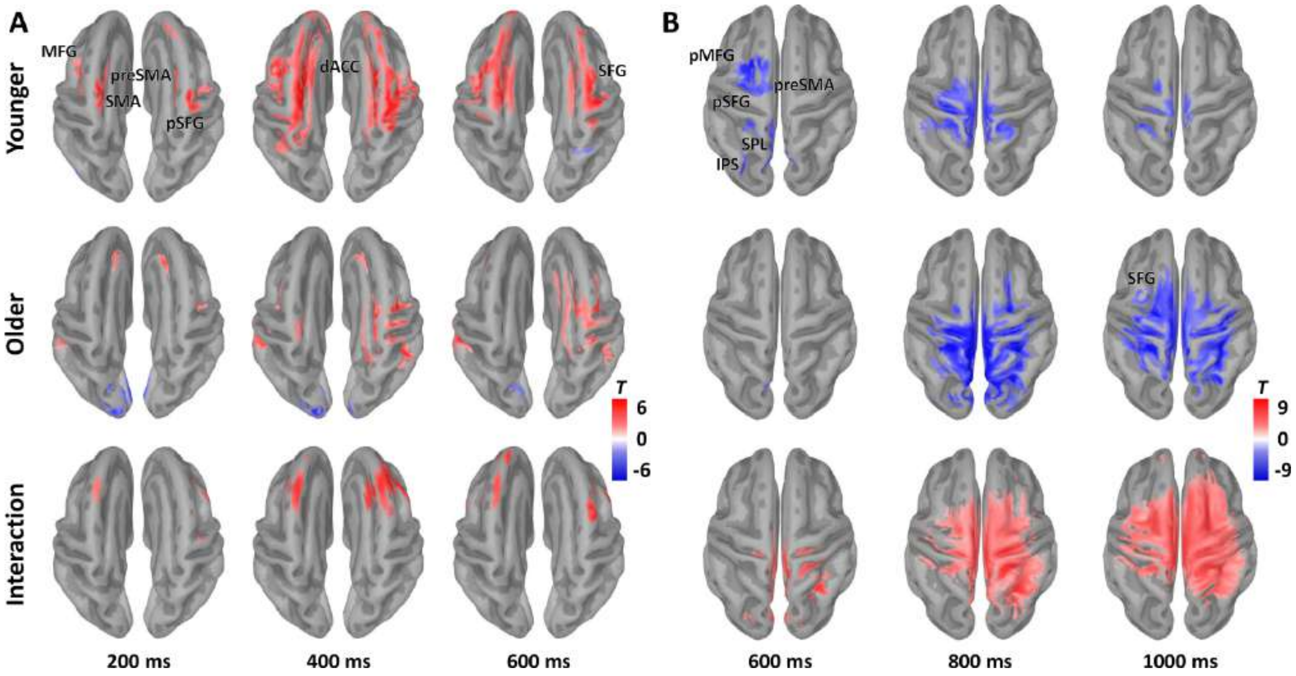

Figure 5 - Results of the source-based event-related spectral perturbation (ERSP) analysis.
The figure shows the cortical distribution for the results of the source-based analysis contrasting incongruent and congruent conditions in younger and older participants for the theta (A) and beta2 (B) frequencies. For illustrative purposes, results for the 5 Hz (A) and 20 Hz (B) frequencies are shown at three representative time points (columns). The topoplots show the *t* values of the significant results. dACC, dorsal anterior cingulate cortex; IPS, intraparietal sulcus; MFG, middle frontal gyrus; pMFG, posterior part of the middle frontal gyrus; preSMA, pre-supplementary motor area; pSFG, posterior part of the superior frontal gyrus; SFG, superior frontal gyrus; SMA, supplementary motor area.

Brain-behaviour correlations

We assessed the significance of the correlations between RT and ERSP Stroop effects over the entire channel-time-frequency space in each age group. We also investigated whether age significantly modulated these brain-behaviour correlations (interaction analysis testing for age-dependent differences in slope). All the results were corrected for multiple comparisons using TFCE method. Still, the interaction analysis revealed a very high number of significant results involving all the frequency bands and generally indicating opposite patterns of brain-behaviour correlations for younger and older participants, with the former showing positive correlation, so that smaller congruency-dependent power differences were related to a better Stroop performance, and the latter showing negative correlations. We will report only the clusters that were significant in this interaction analysis and in (at least) one of the simple correlation analyses for each group. Moreover, for the sake of brevity, we will report in the text only the results for the first 1000 ms after stimulus presentation, a time window that includes approximately 90% and 99% of the valid RTs for older and younger participants, respectively.

A first cluster showing significant age-dependent modulations of the brain-behaviour correlations involved theta and lower alpha frequencies and was distributed over mid-frontal channels in a time window approximately ranging from 150 to 550 ms (see Figure 6). This effect was explained by the fact that, while older participants' ERSP Stroop effects did not significantly explain their behavioural performance, younger participants showed significant positive correlations between RT and ERSP Stroop effects (see Figure 7a). Specifically, younger participants exhibiting a larger behavioural Stroop effect also showed a larger, positive ERSP Stroop effect, that is, greater event-related increases in theta and lower alpha frequencies for the incongruent condition as compared to the congruent one. Similar age-dependent modulations of brain-behaviour correlations – with significant positive correlations between RT and ERSP Stroop effects for younger participants – were found in other partially independent clusters that either involved the same frequencies, but at later time windows and over different scalp locations, or involved beta1 frequencies in an earlier time window (0-300 ms) over left and right centro-temporal channels. Another set of clusters showing a similar age-dependent modulation of the brain-behaviour correlations involved higher frequencies (i.e., >18 Hz) in later time windows (approximately starting from 600 ms) over right parietal and left frontal channels (see Figure 6).

Moreover, the analyses also revealed a cluster of significant age-dependent modulations of the brain-behaviour correlations that showed the opposite pattern of results. That is, in this cluster, the significant age-dependent modulations of the brain-behaviour correlations were due to the fact that older participants showed significant negative correlations between RT and ERSP Stroop effects, while younger participants showed non-significant correlations (with an opposite trend). This cluster involved beta and gamma frequencies and was distributed over left parieto-temporal channels in a time window starting from 450 ms (see Figures 6 and 7b) and, limited to beta1 and beta2 frequencies, over left frontal and central channels in an earlier time window approximately ranging from 350 to 600 ms (see Figure 6). Despite the spatio-temporal distribution of these correlations in the beta-gamma frequencies is different from that observed in the scalp-based ERSP analyses described above (cfr. Figure 3 and 6), it should be noted that the ERSP traces corresponding to these correlations show the same pattern, with a larger power suppression for the incongruent as compared to the congruent condition. Moreover, the pattern of correlations for the age-dependent ERSP effect in the beta band (20 Hz) over Fz described above (see Scalp-based time-frequency and Figure 4) is the same as that described here (see Figure 7b) in a time window ranging from 750 to 900 ms, with older and younger participants showing, respectively, negative and positive correlations between RT and ERSP Stroop effects (*Z*s > 2.02, *p*s < .05).

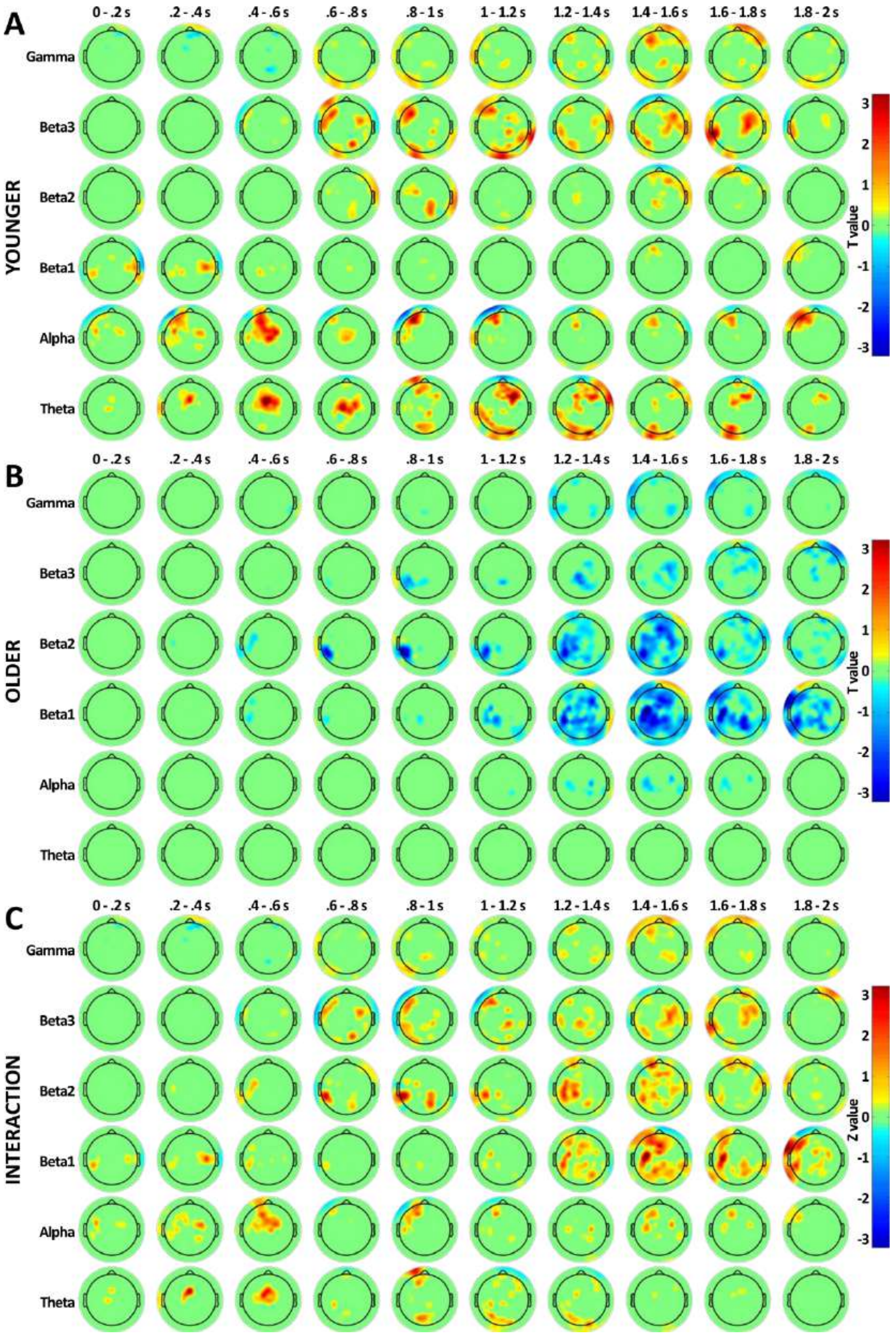

Figure 6 – Brain-behaviour correlation results.

The figure shows the topoplots for the results of the brain-behavior correlation analysis. Specifically, results are shown for the simple effect analysis in younger (A) and older (B) participants, as well as for the interaction analysis (C). Each row represents the average of each frequency band, whereas the columns represents the average of EEG activity every 200 ms after stimulus presentation (time 0). The topoplots show the *t values* of the significant results after TFCE.

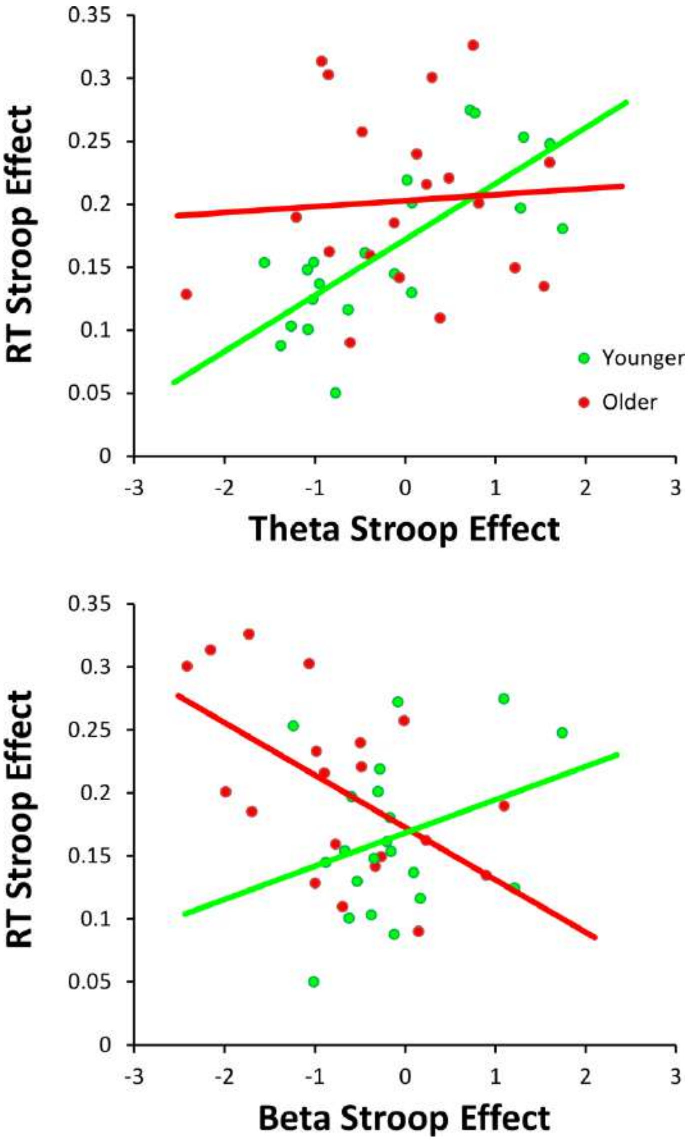

Figure 7 – Representative results of the brain-behaviour correlation analysis.
The scatterplots show the correlation between the behavioural Stroop effect (*y* axis) and the ERSP Stroop effect for the younger and older groups (light green and red points, respectively; regression lines are also shown in the same colours). The scatterplot in (A) depicts representative data for a frequency in the theta band (7 Hz) extracted from a channel in the mid-frontal cluster (FCz) at 500 ms, for which the brain behaviour correlation was significantly different between the two age groups ($Z = 3.46$, $p < .001$). The scatterplot in (B) depicts representative data for a frequency in the beta2 band (20 Hz) extracted from a channel in the left parieto-temporal cluster (near T7) at 850 ms, for which the brain behaviour correlation was significantly different between the two age groups ($Z = 3.70$, $p < .001$) (see text for details).

Discussion

In this study, we investigated the spectral correlates of interference control and their age-related differences. To this purpose, we recorded EEG activity from two age groups and analysed time-frequency dynamics, estimating the underlying neural sources. Furthermore, we also aimed at testing the hypothesis that this cognitive process relies on the left portion of PFC, as suggested by previous studies (Stuss and Alexander, 2007).

Our results revealed a main role of beta2 frequencies (19-24 Hz) and left PFC in younger participants, which may underlie the process of selecting task-relevant representations during interference control. We found clear age-related differences, since older participants showed a delayed (600-800 ms) over-recruitment of higher frequencies bands (from beta1 to gamma) with bilateral brain areas involved. The main finding from the correlation analysis concerned a positive correlation between RTs and midfrontal theta that was present for the younger participants only and that can be considered as a signal for the need for cognitive control (Cavanagh and Frank, 2014).

In terms of behavioural analysis, we found that all participants showed longer RTs and lower accuracy in responding to incongruent trials. Moreover, older participants showed a general trend in responding more slowly to both types of trials, but they did not show any difference in accuracy as compared to younger participants. These results are in line with general slowing accounts, which proposed that older adults are slower in responding especially when the task requires to select a stimulus (i.e., ink colour/arrow direction) over a more dominantly represented one (i.e., word reading/arrow location), as in the case of Stroop paradigms (Salthouse, 1996; Verhaeghen and De Meersman, 1998). However, older adults also displayed a stronger Stroop effect for RTs when compared to the younger group, which indicated that they are even slower in responding to the incongruent trials and more subjected to the cognitive interference. Note that the logarithmic transformation we applied to RTs mitigates the near-multiplicative slowing effects commonly observed in aging research (Cerella, 1990; Faust et al., 1999). Based on this evidence, together with our electrophysiological results, we suggest that slowing of processing speed is not the only explanation for the age-related difference in Stroop performance.

At the electrophysiological level, we found a major event-related modulation of beta2 (19-24 Hz) frequencies in the younger group, which was localized on prefrontal regions in a relatively early time window (400-600 ms). When we examined the power time series, we found a stronger suppression of these frequencies for incongruent trials compared to congruent ones. By contrast, the pattern for older participants revealed a later, widespread modulation involving all beta (13-30 Hz) and gamma (31-45 Hz) frequencies on most electrodes spread over the scalp. In particular, the

ERSP Stroop effect for older adults was evident in a later time window for these frequencies and channels due to a more sustained power suppression for incongruent trials. We propose that this pattern of age-related differences may indicate that prefrontal beta2 frequencies would be specifically implicated in interference control processing but, at an older age, this specificity is lost, and other frequency bands and cortical regions are additionally recruited, in line with the dedifferentiation theories of aging (Reuter-Lorenz and Park, 2014).

In the light of recent works posing attention on the cognitive meaning of beta frequencies, we interpreted our beta band activation as a cognitive marker of interference control, probably involved in the selection of task-relevant representation (Antzoulatos and Miller, 2016; Spitzer and Haegens, 2017). Previous functional magnetic resonance imaging (fMRI) studies using Stroop paradigms reported evidence compatible with this hypothesis suggesting that conflict resolution is achieved thorough a mechanism involving the amplification of task-relevant representation (Banich, 2009; Egner and Hirsch, 2005). Indeed, according to our source results, the incongruency-dependent beta2 power modulations seem to be generated especially from posterior portions of the left middle and superior frontal gyri (pMFG, pSFG) engaged after stimulus presentation. This is in agreement with the model proposed by Banich (2009) where the middle portion of DLPFC is recruited to bias the selection of the relevant representation. Moreover, our results from younger participants confirmed previous findings suggesting that left prefrontal cortex mediates interference control through the process of selection of task-relevant rules (Derfuss et al., 2005; Stuss, 2011; Stuss and Alexander, 2007; Vallesi, 2012). They are also in line with those of a previous study linking beta band activity, and in particular its left lateralization, on MFG with Stroop performance, which showed that a stronger left lateralization of prefrontal of beta spectral activity at rest correlated with a smaller Stroop effect and better capacity to resist to the interference (Ambrosini and Vallesi, 2017).

Albeit we cannot exclude that motor processes contributed to explain our results involving the beta band, we think that they could not be just explained as mere correlates of motor outcomes. First, we found the power suppression mainly on the left hemisphere, despite the task required a bimanual response, and the results from the source estimation did not show involvement of the primary hand motor areas. Second, despite we did not perform response-locked ERSP analyses, the pattern of the event-related decrease in high frequency power is not compatible with the pattern of RTs. Indeed, despite older participants' RTs were slower in both conditions, and especially in the incongruent one (see Figure 2), the maximum decrease in beta power was observed at around the same time for both age groups and for both congruent and incongruent trials. Rather, the decrease in beta power for incongruent as compared to congruent condition was more sustained for older participants, causing the ERSP Stroop effect to occur later in this age group (see Figure 4a, b). Third, even if we assume that the temporal differences in the ERSP Stroop effects between the two age groups could be explained by the RT slowing shown by older participants, this can hardly explain the age-dependent spatial and spectral over-recruitment we found. Fourth, the suppression of beta (15-30 Hz) power that is usually observed before and during the execution of voluntary movements should be i) accompanied by a similar suppression of mu (8-14 Hz) power and ii) followed by the so-called beta rebound, a post-movement increase in beta power. However, no beta rebound was evident in our data (see Figure 4a) and the frequencies in the mu band showed an event-related increase in power, rather than suppression, especially in younger participants (see Figure 3).

Indeed, concerning the results for older adults, we found an over-recruitment of beta and gamma bands. Specifically, the source-based ERSP analysis revealed that older participants showed a more widespread ERSP Stroop effect in the beta2 frequencies, as compared to younger ones, which involved extended portions of bilateral dorsal frontal and parietal cortices without any sign of hemispheric asymmetry. This result is consistent with other studies reporting an age-related overactivation and reduction in hemispheric specialization, or a general dedifferentiation of neural processing (Cabeza, 2002; Goh, 2011; Park and Reuter-Lorenz, 2009; Reuter-Lorenz and Park, 2014). To specifically select task-relevant information and ignore irrelevant and dominantly represented one, as required in the Stroop task, is a demanding function. Therefore, it is possible that, with aging, a restricted spectrum of frequencies (such as beta2 for younger participants) may be no longer enough to carry out this function, and that this may recruit more electrophysiological resources in terms of both frequencies and neural sources. Moreover, older participants not only showed a spatio-spectral over-recruitment of neural resources, but also a more sustained power suppression for incongruent trials. Again, these results seem to be in line with theories suggesting that aging is related to a so-called dedifferentiation (Reuter-Lorenz and Park, 2010, 2014). Finally, the recruitment of medial portions of the frontal cortex (i.e., dACC) in older participants is also consistent with this idea, as well as with the predictions of the Cascade of Control model (Banich, 2009) and with findings of older adults showing increased activity in the cingulate cortex during a Stroop task (Milham et al., 2002). Thus, our results can be considered as further evidence that oscillatory dynamics are sensitive to age.

The source-based time-frequency analysis also showed age-dependent differences in theta ERSP Stroop effects over dorsomedial and dorsolateral prefrontal cortices for younger as compared to older participants, for whom this effect was virtually absent. Even if this result was not reflected in the scalp-based analysis, it indicates an age-dependent impairment of the theta-related mechanism signalling the need of cognitive control, that is, an early process that, based on the current contextual information, signals that cognitive control processes are needed to cope with the Stroop interference. This interpretation is in line with a large body of findings suggesting that midfrontal theta activity may be a marker that signals the need for cognitive control (Cavanagh and Frank, 2014; Cohen, 2014; Nigbur et al., 2011; Sauseng et al., 2010). Moreover, we also found an age-dependent difference in the correlation between the Stroop effect in RT and that in theta power over midfrontal regions as soon as 150 ms after stimulus presentation, which emerged from interaction results but was due to younger participants only. Indeed, younger participants exhibiting a larger behavioural Stroop effect also showed a larger, positive ERSP Stroop effect, that is, greater event-related increases in theta (and lower alpha) frequencies for the incongruent condition as compared to the congruent one, and this correlation was significantly different from the non-significant one observed in older participants (Figure 7a). Given the proposed role of midfrontal theta as a marker for the need of cognitive control (Cavanagh & Frank, 2014; Cohen, 2014), our results for the theta frequencies would suggest that this function may change during the adult lifespan. Finally, these results are in line with recent findings showing that older adults are less capable to detect interference than the younger ones, as evidenced by a decrease in mid-frontal theta power effects, and thus lack early interference detection signals (Ferreira et al., 2019).

Conclusions

To the best of our knowledge, this is the first study investigating oscillatory dynamics in spatial conflict processing with groups of different ages. Our results highlighted that, during the adult lifespan, neural oscillations show age differences mainly reflected in the impairment of theta-related cognitive processes signalling the need of control and an over-recruitment over frequencies and brain areas. We hypothesized that these age-dependent differences may contribute to the decline commonly observed in cognitive aging. Of course, this interpretation should be corroborated with a longitudinal approach. Future studies should also address the issue of causal involvement of specific neural correlates in interference control process, for example, through neurostimulation techniques. Shedding light on these mechanisms would also help designing neuromodulation therapies for clinical population and reducing the cognitive decline observed in healthy aging.

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