

Effects of reaction time variability and age on brain activity during Stroop task performance

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Abstract Variability in reaction time during task performance may reflect fluctuations in attention and cause reduced performance in goal-directed tasks, yet it is unclear whether the mechanisms behind this phenomenon change with age. Using fMRI, we tested young and cognitively healthy older adults with the Stroop task to determine whether aging affects the neural mechanisms underlying intra-individual reaction time variability. We found significant between-group differences in BOLD activity modulated by reaction time. In older adults, longer reaction times were associated with greater activity in frontoparietal attentional areas, while in younger adults longer

reaction times were associated with greater activity in default mode network areas. Our results suggest that the neural correlates of reaction time variability change with healthy aging, reinforcing the concept of functional plasticity to maintain high cognitive function throughout the lifespan.

Keywords Aging · fMRI · Attention · Reaction time · Performance variability

Introduction

A large body of literature has demonstrated that attention declines with age (Madden 2007; Spieler, Balota, and Faust 1996; Verhaeghen and Cerella 2002), which suggests that maintaining attention during goal-directed tasks may become more difficult with age. Two brain networks have been shown to be important in the performance of goal-directed tasks: the frontoparietal attentional network and the default mode network (DMN). Age-related changes in attention are accompanied by increased activity in the frontoparietal attentional network as revealed by visual tasks assessing top-down attention in older adults (Corbetta and Shulman 2002; Madden et al. 2007). Frontal areas, including the inferior frontal gyrus, middle frontal gyrus, and superior frontal gyrus, also demonstrate increased activity in older adults during selective attentional tasks (Langenecker, Nielson, and Rao 2004; Milham, Erickson, Banich, and Kramer 2002; Zysset, Schroeter, Neumann, and Yves von Cramon 2007). These age-related increases in activity are often considered compensatory brain mechanisms to facilitate cognitive performance, allowing older adults to perform equivalently to younger adults, particularly during tasks with low cognitive load (Cabeza, Anderson, Locantore, and McIntosh 2002; Davis, Kragel, Madden, and Cabeza 2012; Reuter-Lorenz et al. 2006). Age-related changes in frontoparietal regions are relevant because

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temporary decreases in frontoparietal activity can predict task errors and degree of distraction in younger adults (Leber 2010; Padilla, Wood, Hale, and Knight 2006), but whether that pattern of neural activity is similar in older adults remains to be discovered.

The DMN, which also mediates goal-directed task performance, consists of a set of brain regions that show greater activity during rest and decreased activity during goal-directed tasks (Buckner, Andrews-Hanna, and Schacter 2008; Damoiseaux et al. 2006; Raichle et al. 2001). In fact, activity within the DMN can vary parametrically with task difficulty (McKiernan, Kaufman, Kucera-Thompson, and Binder 2006). Like the frontoparietal attentional network, activity in this network becomes altered throughout aging. During rest, older adults show less DMN activity and coactivation between DMN regions compared to younger adults (Damoiseaux et al. 2008; Wu et al. 2011). By contrast, during task performance, older adults show greater DMN activity compared to younger adults (Grady, Springer, Hongwanishkul, McIntosh, and Winocur 2006; Lustig et al. 2003; Miller et al. 2008). This is important because greater activity in DMN regions has been linked to errors in a sustained attention task (Bonnelle et al. 2011; Christoff, Gordon, Smallwood, Smith, and Schooler 2009).

These studies suggest that activity within the DMN and the frontoparietal attentional network may be able to predict attentional fluctuations, as defined by changes in reaction times. This has been found to be the case. In a study that examined the neural bases of attentional fluctuations in young adults, the authors found a positive relationship between longer reaction times and peak target-related activity in DMN regions (Weissman, Roberts, Visscher, and Woldorff 2006). The authors also found that decreased activity in areas of the frontoparietal attentional network predicted longer reaction times (Weissman et al. 2006).

In the present study, we aimed to analyze how brain activity that varies as a function of reaction time changes with age during an attention task. Specifically, we used functional magnetic resonance imaging (fMRI) to examine brain activity in young and cognitively healthy older adults while they performed a trial-by-trial Stroop task in which we recorded their reaction time to each stimulus. We chose the Stroop task because of its simplicity to administer and its ability to engage and challenge participants' attention. In this task, participants are asked to identify the ink color in which a word is presented (e.g. "blue" presented in red ink), regardless of the word's semantic meaning. The semantic meaning of the word can compete with the ink color, resulting in interference in task performance where participants are slower at naming the ink color when the semantic meaning is incongruent with the ink color (e.g. "blue" presented in red ink), compared to conditions when the semantic meaning is congruent (e.g. "blue" presented in blue ink) or neutral (e.g. "house" presented in

blue ink) with the ink color (Stroop 1935). In terms of age effects on behavior in the Stroop task, previous studies report contradictory results, where some report no significant differences in reaction times (Langenecker et al. 2004; Milham et al. 2002), accuracy rates (Milham et al. 2002), or interference (Verhaeghen and De Meersman 1998) between young and older adults, while others report older adults have longer reaction times (Zysset et al. 2007) and experience greater interference (Spieler et al. 1996). Previous work on age effects on the neural correlates of the Stroop task has characterized prefrontal hyperactivation in older adults in the context of inhibition and conflict processing (Laguë-Beauvais, Brunet, Gagnon, Lesage, and Bherer 2013; Langenecker et al. 2004; Mathis, Schunck, Erb, Namer, and Luthringer 2009; Milham et al. 2002; Schulte et al. 2011). However, unlike those previous studies, we used this paradigm to examine the neural correlates underlying intra-individual reaction time variability.

We wanted to explore whether task-related brain activity that varies with reaction time changes with age. Given the previous literature, we hypothesized longer reaction times would be preceded by greater activity in DMN regions and decreased activity in frontoparietal attentional regions in both young and older adults. We also expected activity in these regions to vary proportionally with response time to stimuli. In addition, we expected age-related changes in reaction time-modulated activity, specifically that older adults would demonstrate greater baseline, or pre-stimulus, activity in frontoparietal regions preceding longer reaction times, compared to young adults in accordance with compensatory models of cognitive aging (Cabeza 2002; Reuter-Lorenz and Cappell 2008). We also expected pre-stimulus activity in DMN regions preceding longer reaction times to be greater in older adults. In line with previous Stroop studies, we predicted participants would have longer reaction times during the incongruent condition relative to the congruent and neutral conditions. Our findings revealed that older adults exhibit altered brain activity in areas within the frontoparietal attentional and default mode networks that contribute to reaction time variability, which may help to maintain efficient levels of attention in order to perform goal-directed tasks.

Methods

Participants

Fifteen young adults and twenty-eight cognitively normal older adults were recruited from the community and gave written informed consent prior to study participation (see Table 1 for demographics and behavioral performance data). Participants were English speakers, had normal color vision, and had normal or corrected-to-normal vision. Individuals who could not meet the MRI safety standards were excluded.

Table 1 Participant characteristics and behavioral performance

	Young	Older
n	15	28
Age	23.5±1.6	64.8±8.7
Sex (male:female)	6:9	11:17
Years of education	17.2±1.0	15.9±3.4
Incongruent RT (ms)	684.6±144.6	747.7±116.7
Congruent RT (ms)	567.5±123.2	607.8±98.0
Neutral RT (ms)	605.9±119.7	643.8±91.6
Overall error rate (%)	3.9±2.8	3.7±4.1

Values for continuous variables are means followed by standard deviation

Individuals who had a history of neurological conditions (e.g. stroke) or a family history of early onset Alzheimer's disease were also excluded. The study was approved by the Queen's University Research Ethics Board.

All participants underwent a battery of neuropsychological tests to ensure cognitive normality. Global functioning was assessed with the Montreal Cognitive Assessment (MoCA) and the Mattis Dementia Rating Scale. Verbal memory was assessed with the California Verbal Learning Test Version II (CVLT-II). Executive function and attention were measured with the Wisconsin Card Sorting Test, the Trail Making Test B, and the paper version of the color-word Stroop task. All participants had to score within normal range (above -1.5 standard deviations), adjusted for age, sex, and years of education, in all tests for inclusion.

Behavioral task

The behavioral task used within the MRI scanner was a rapid event-related adaptation of the color-word Stroop paradigm. Before the experiment, participants underwent a brief training session to familiarize them with the task. A computer was used to display stimuli and to record participants' responses. Stimuli were presented through back projection onto a screen that was viewed on a mirror attached to the head coil of the scanner.

The color-word stimuli used in the task were red, green, yellow, and blue. We included three trial types: congruent, incongruent, and neutral. Congruent stimuli were color words written in the same ink color (e.g. BLUE written in blue). Incongruent stimuli were color words written in a different ink color (e.g. BLUE written in red). Neutral stimuli were non-color words also written in the four ink colors (e.g. HOME written in yellow). The neutral words used in the experiment were "home", "chair", "day", and "finger". The word frequency of the neutral words was balanced. The character lengths of the neutral word also matched the lengths of the color-word stimuli.

The experiment consisted of 7 runs within a single scanning session. For the duration of each run, participants were asked to identify as fast as possible the color of the ink in which the word was written. Vocal responses were recorded with an MR compatible microphone that was attached to the head coil of the scanner. Each stimulus appeared against a black screen for 1,000 ms. A white fixation cross was displayed throughout each run during inter-trial intervals. The inter-trial intervals were randomly jittered and ranged from 1 to 19 s. The random stimulus sequence and jittering was generated with Optseq (<http://surfer.nmr.mgh.harvard.edu/opt-seq/>). Each run contained 15 stimuli of each trial type, for a total of 45 stimuli in each run. This yielded a total of 105 stimuli of each trial type for a total of 315 stimuli across all 7 runs. Each run lasted 4 min and 12 s, and there was a brief break between each run.

Verbal responses to the event-related Stroop task were scored for performance accuracy and reaction times (RTs). Only correct responses were included in the functional analyses, thereby excluding errors, missed, incorrect-then-corrected, and unintelligible responses from the fMRI analyses. Excluded responses constituted 3.81 % of all responses. The z-scores for all RTs to correct responses were calculated for each individual as follows: (RT trial – individual mean RT for that trial type) / (individual RT standard deviation for that trial type). These RT z-scores were later used as weights for our parametric regressors in our general linear model.

Imaging procedures

Imaging was performed using a 3-T Siemens Magnetom Trio MRI system (Siemens Medical Systems, Erlangen, Germany) with a 12-channel head coil at the Queen's University Research MRI Facility. A 176-slice high-resolution anatomical scan was acquired using a T1-weighted 3D MP-RAGE sequence ($TR=1,760$ ms, $TE=2.2$ ms, flip angle= 9° , $FOV=256$ mm, voxel size= 1 mm³). During the performance of each run of the event-related Stroop task, 125 BOLD images were acquired using T2*-weighted gradient EPI along the anterior commissure-posterior commissure (AC-PC) line (32 axial slices, $TR=2,000$ ms, $TE=30$ ms, flip angle= 78° , $FOV=211$ mm, voxel size= 3.3 mm³).

fMRI data preprocessing

fMRI data were analyzed using BrainVoyager QX (Brain Innovation, Maastricht, the Netherlands). The first two volumes of each functional run were discarded to allow the MR signal to reach a steady state. Prior to statistical analyses, all functional images underwent 3D motion correction (six parameter rigid transformation including 3 rotations and 3 translations), slice scan time correction, and high-pass temporal filtering (removing frequencies below three cycles per time

course). To minimize motion artifacts as much as possible, a cut-off criterion for excluding functional runs where subjects made 3.3 mm or larger head movements was implemented. Excluded runs constituted 9.997 % of all functional runs. To further account for the possible effects of the head movements that passed the cut-off criterion, the six head movement parameters were added into the design matrices as confound predictors. Functional images were co-registered with the anatomical scans and transformed into Talairach coordinate space (Talairach and Tournoux 1988). Images were spatially smoothed with a full-width at half maximum Gaussian kernel of 8 mm.

fMRI data analysis

The time series for each functional run was analyzed using a deconvolution approach, which implements a finite impulse response model, to our general linear model (GLM) that was corrected for serially autocorrelated observations. The linear model included 10 regressors, spanning 10 TRs (20 s), to model the average stimulus-locked BOLD response for each trial type. The six motion correction regressors were also included in the GLM. Ten additional parametric regressors for each trial type were included to determine whether and how the magnitude of the BOLD response varied with RT. These parametric regressors were weighted with the RT z-score for each correct response. It is important to highlight that each condition was z-scored to remove the interference effect of the incongruent condition. In this way the reaction time variations between the three conditions (congruent, neutral and incongruent) were weighted the same, regardless of the raw reaction time differences (e.g. larger RT for incongruent trials than for congruent trials).

Thus, in our GLM, for each trial type, we included 20 regressors: 10 regressors to model the average BOLD response and 10 parametric regressors to model the variance in the BOLD response that varied with RT z-scores. Due to the sluggishness of the hemodynamic response, we assumed that the peak of the stimulus-activated BOLD response would occur four to six seconds after presentation of the stimulus. Therefore, we assumed the first and second regular and parametric regressors (which correspond to the beginning of the first and second TR after stimulus presentation) modeled pre-stimulus BOLD activity while the third and fourth regular and parametric regressors (which correspond to the beginning of the third and fourth TR after stimulus presentation) modeled the peak stimulus-activated BOLD response. This parametric deconvolution method of analysis has been successfully applied in a study by Weissman et al. (Weissman et al. 2006).

We performed three analyses: separate within-group analyses for young and older adults and an analysis of the two groups combined to test for group-by-task interactions to examine age effects. We tested the main effect of the

parametric regressors to determine brain regions that display pre-stimulus BOLD signal changes that vary with reaction time. Regions of interest (ROIs) were functionally defined from all resulting statistical maps. Each ROI was a 1000-voxel cube centered on a local maximum in a statistical map. The time courses of each ROI were then extracted. Statistical significance was set a threshold of $q < 0.05$, using the false discovery rate (FDR) to correct for multiple comparisons.

Results

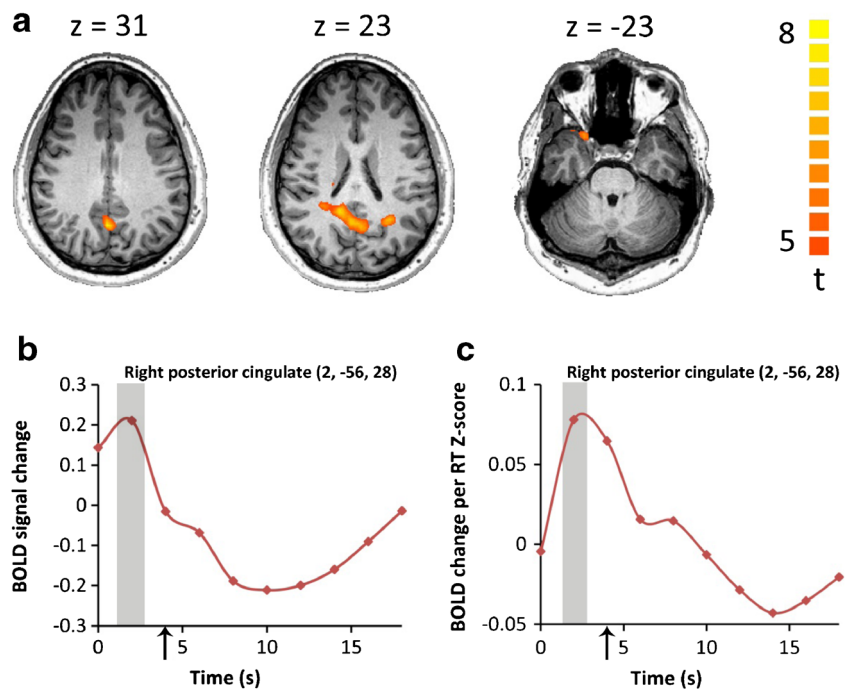
Behavioral results

A mixed ANOVA revealed a main effect of condition on RT ($F_{2,41} = 109.68$, $\eta^2 = 0.728$, $p < 0.001$). Consistent with results from previous Stroop studies, post-hoc t-tests revealed the mean incongruent RT (725.6 ± 129.0 ms) across all participants was significantly greater than the mean RTs for congruent and neutral trials (593.7 ± 107.8 ms and 630.6 ± 102.5 ms respectively; $t_{42} = 13.06$, $d = 1.99$ for incongruent vs congruent and $t_{42} = 12.03$, $d = 1.83$ for incongruent vs neutral; both $p < 0.001$). The mean RT for neutral trials across all participants was also significantly greater than the mean congruent RT ($t_{42} = 5.04$, $d = 0.768$, $p < 0.001$). The ANOVA did not reveal a significant main effect of age ($F_{1,41} = 1.86$, $\eta^2 = 0.043$, $p = 0.18$) nor a significant interaction between condition and age ($F_{2,41} = 1.21$, $\eta^2 = 0.029$, $p = 0.30$) on RT, suggesting that young and older adults performed equivalently to each other across all congruent, incongruent, and neutral conditions (see Table 1 for behavioral data). Participants performed the Stroop task across all conditions with very few errors (mean error rate = 3.8 %). A mixed ANOVA revealed a main effect of condition on error rates ($F_{2,41} = 9.24$, $\eta^2 = 0.184$, $p < 0.001$). Post-hoc pairwise comparisons revealed the incongruent error rates (5.19 ± 0.69 %) were significantly higher than the congruent and neutral error rates (3.40 ± 0.66 % and 3.41 ± 0.66 % respectively; $t_{42} = 3.39$, $d = 0.518$ for incongruent vs congruent and $t_{42} = 3.06$, $d = 0.466$ for incongruent vs neutral; both $p < 0.005$). The ANOVA did not reveal a significant main effect of age ($F_{1,41} = 0.27$, $\eta^2 = 0.006$, $p = 0.61$) nor a significant interaction between condition and age ($F_{2,41} = 2.05$, $\eta^2 = 0.048$, $p = 0.14$) on error rates.

fMRI results

Several regions throughout the brain displayed BOLD activity that varied with RT in both young and older adults (Figs. 1, 2, and 3). As predicted, greater pre-stimulus BOLD activity in the DMN was found to be associated with longer RTs (Supplementary Table 1). Young adults exhibited BOLD responses

Fig. 1 **a** Areas that exhibit increased pre-stimulus BOLD activity with longer reaction times in young adults. Images are presented in radiological convention and thresholded at $q < 0.05$, FDR corrected. **b** Average BOLD response to target stimuli in the right posterior cingulate (2, -56, 28). **c** Average BOLD response influenced by RT z-scores in the right posterior cingulate (2, -56, 28). At 2 s (*shaded area*), and thus before stimulus onset as the hemodynamic response (marked by *black arrow*) is lagged by 4–6 s, the BOLD response increases with larger z-scores, and therefore longer RTs. This pattern of activity was consistent among all regions listed in the Young portion of Supplementary Table 1



that increased proportionally with RT in the bilateral posterior cingulate, left inferior frontal gyrus, and left middle temporal gyrus (Fig. 1). Older adults displayed this activity in the bilateral precuneus, bilateral parahippocampal gyrus, and left medial frontal gyrus (Fig. 2).

Older adults displayed decreased pre-stimulus BOLD activity with longer RTs in several regions, including areas related to attention such as the anterior cingulate, superior

temporal gyrus, and inferior frontal gyrus (Fig. 3, Supplementary Table 2). By contrast, in young adults, no regions were found to show significant decreases in activity with longer RTs.

Several areas were found to be significantly different between young and older adults, mainly the inferior frontal gyrus, medial frontal gyrus, parahippocampal gyrus, and the posterior cingulate (Figs. 4 and 5, Supplementary Table 3).

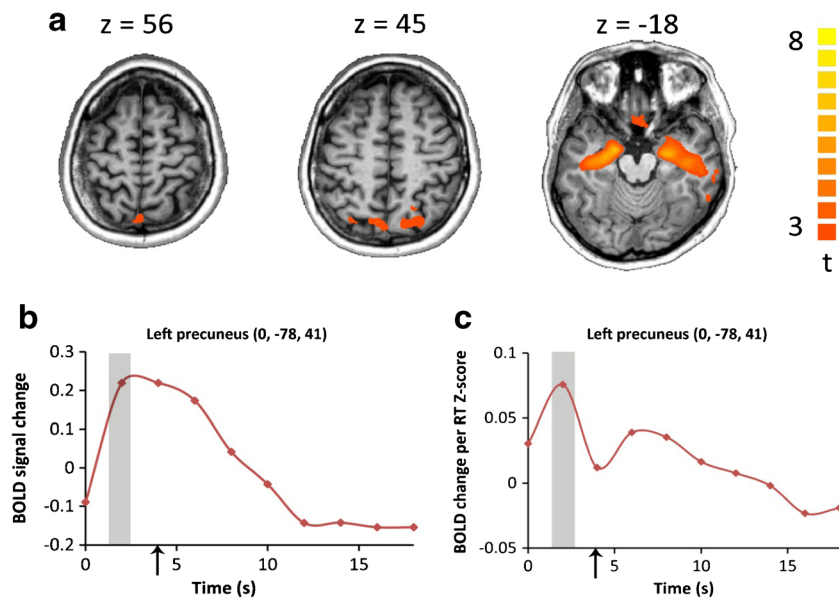


Fig. 2 **a** Areas where pre-stimulus BOLD activity varies positively with reaction times in older adults. Images are presented in radiological convention and thresholded at $q < 0.05$, FDR corrected. **b** Average BOLD response to target stimuli in the left precuneus (0, -78, 41). **c** Average BOLD response influenced by RT z-scores in the left precuneus (0, -78,

41). At 2 s (*shaded area*), and thus before stimulus onset as the hemodynamic response (marked by *black arrow*) lags by 4–6 s, the BOLD response increases with larger z-scores, and therefore longer RTs. This pattern of activity was consistent among all regions listed in the Older portion of Supplementary Table 1

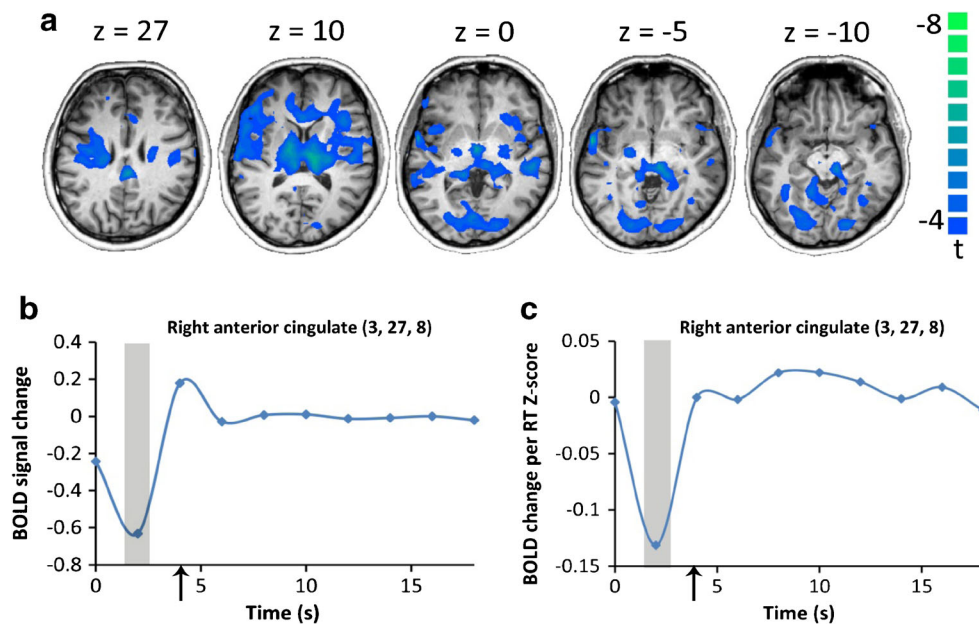


Fig. 3 **a** Areas where pre-stimulus BOLD activity varies negatively with reaction times in older adults. Images are presented in radiological convention and thresholded at $q < 0.01$, FDR corrected. **b** Average BOLD response to target stimuli in the right anterior cingulate (3, 27, 8). **c** Average BOLD response influenced by RT z-scores in the right anterior

cingulate (3, 27, 8). At 2 s (*shaded area*), and thus before stimulus onset as the hemodynamic response (marked by *black arrow*) lags by 4–6 s, the BOLD response decreases with larger z-scores, and therefore longer RTs. This pattern of activity was consistent among all regions listed in the Older portion of Supplementary Table 2

ROI analyses revealed areas in which pre-stimulus BOLD activity was positively modulated by reaction time in young, but not older, adults, which included frontal attentional and default mode regions (Fig. 4a, Supplementary Table 3) (for all areas, $t_{41} \geq 3.00$, $q < 0.05$, $p < 0.05$); Fig. 4c shows this effect in

the posterior cingulate as an example. ROI analyses also revealed areas in which pre-stimulus BOLD activity was positively modulated by reaction time in older, but not young, adults, which were located mainly in the frontal lobes (Fig. 5a, Supplementary Table 3) (for all areas, $t_{41} \geq 2.00$, $q < 0.05$,

Fig. 4 **a** Areas in which pre-stimulus activity positively varied with RT in young adults, but not in older adults. Images are presented in radiological convention and thresholded at $q < 0.01$, FDR corrected. **b** Average BOLD responses to target stimuli in the right posterior cingulate (20, -53, 18). **c** Average BOLD responses influenced by RT z-scores in the right posterior cingulate (20, -53, 18). At 2 s (*shaded area*), and thus before stimulus onset as the hemodynamic response (marked by *black arrow*) lags by 4–6 s, the BOLD response increases with larger z-scores, and therefore longer RTs, in young adults but not in older adults. This differentially modulated activity was consistent among all regions listed in the Young > Older portion of Supplementary Table 3

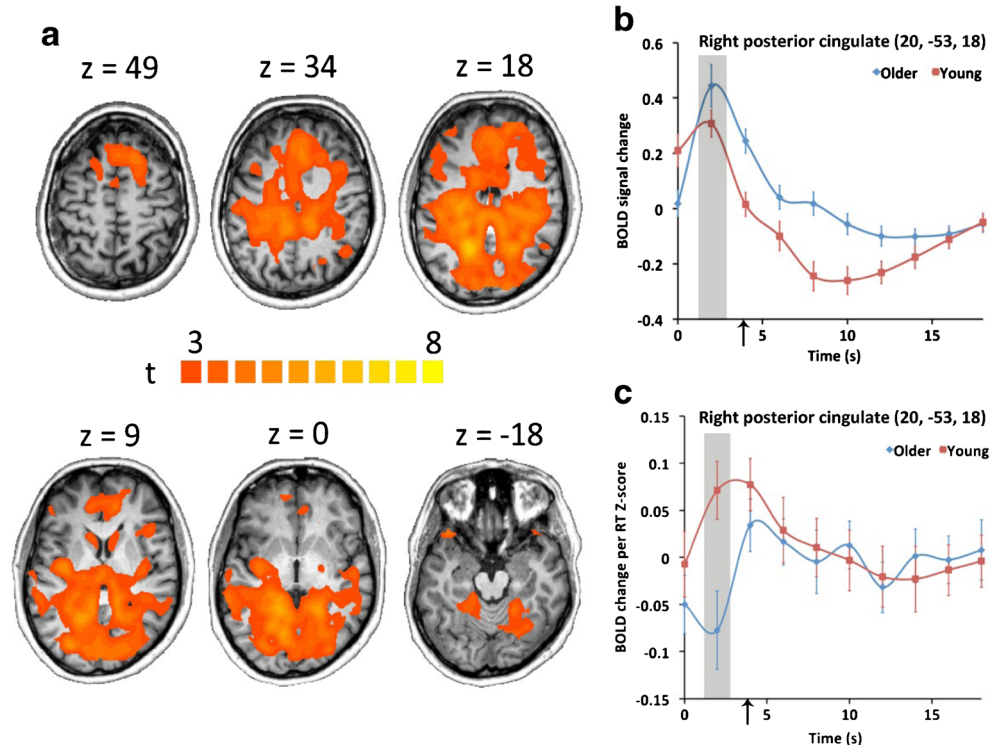
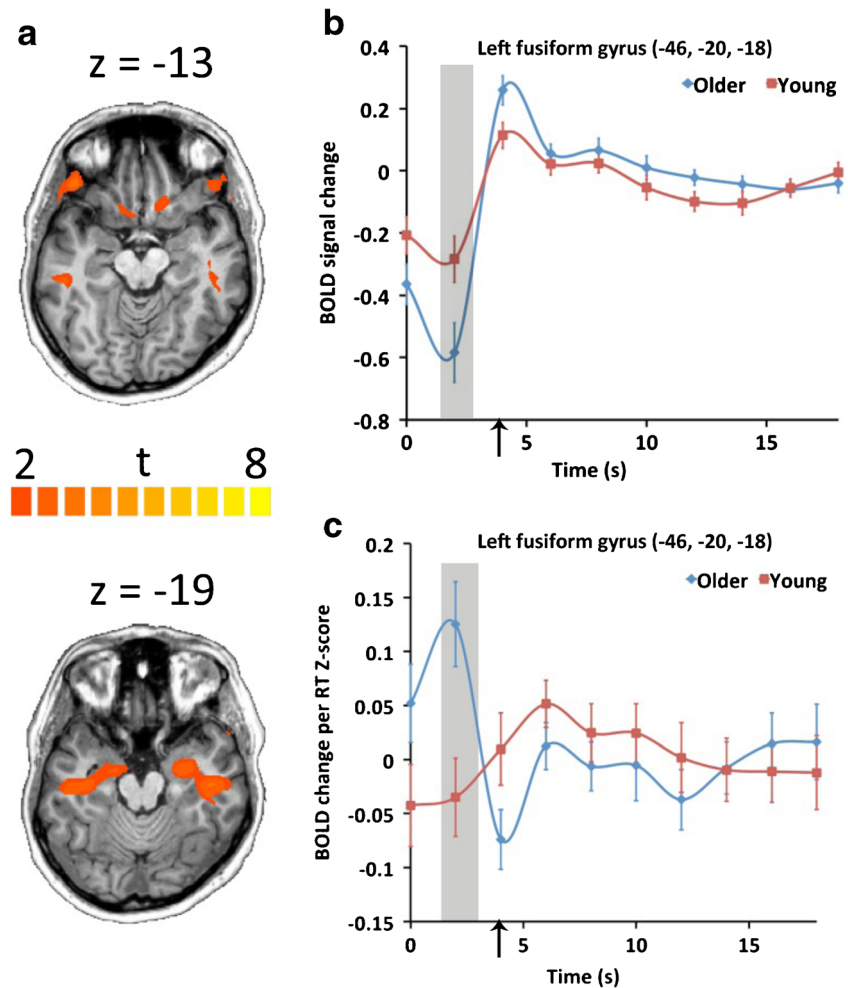


Fig. 5 **a** Areas in which pre-stimulus activity positively varied with RT in older adults, but not in young adults. Images are presented in radiological convention and thresholded at $q < 0.05$, FDR corrected. **b** Average BOLD responses to target stimuli in the left fusiform gyrus (-46, -20, -18). **c** Average BOLD responses influenced by RT z-scores in the left fusiform gyrus (-46, -20, -18). At 2 s (shaded area), and thus before stimulus onset as the hemodynamic response (marked by black arrow) lags by 4–6 s, the BOLD response increases with larger z-scores, and therefore longer RTs, in older adults but not in young adults. This differentially modulated activity was consistent among all regions listed in the Older > Young portion of Supplementary Table 3



$p < 0.05$); Fig. 5c shows this effect in the fusiform gyrus as an example.

Regarding mean unmodulated activation maps for each condition, older adults displayed activity in the temporal pole and middle temporal gyrus in all three conditions and additional activity in the anterior cingulate, precentral gyrus, and frontal lobes in the incongruent condition (Supplementary Fig. 1). The younger adults displayed similar patterns of activity as the older group, such as anterior cingulate activity in the incongruent condition, but to a lesser extent (Supplementary Fig. 2). When contrasting the older and younger adults against each other, in the incongruent condition, older adults showed greater activity in the posterior cingulate, precentral gyrus, inferior frontal gyrus (pars triangular), and the temporal lobe, while younger adults showed increased activity in the isthmus of the cingulate/restrosplenial cortex (Supplementary Fig. 3a). For the congruent condition, older adults displayed greater activity in the insula and temporal pole, while young adults displayed greater activity in the extrastriate visual cortex (Supplementary Fig. 3a). Finally in the neutral condition, older adults showed increased activity in

the frontal lobe, notably in the orbitofrontal cortex and pars triangular part of the inferior frontal gyrus, and the temporal lobe compared to young adults (Supplementary Fig. 3a).

Discussion

In this study, we identified several brain regions that contribute to RT variability in young and older adults. These regions were related to the frontoparietal attentional system and the DMN. Consistent with our hypothesis, we found longer response times were associated with greater pre-stimulus activity in DMN regions. As expected, we also found that longer RT coincided with decreased pre-stimulus activity in frontoparietal attentional regions. Finally, we found that reaction time-modulated activity changes with age.

That greater activity in DMN regions was associated with slower responses may indicate more mind wandering occurred during attentional lapses relative to faster responses, supporting previous research on DMN activity and mind

wandering (Andrews-Hanna, Reidler, Huang, and Buckner 2010; Christoff et al. 2009; Mason et al. 2007). Longer reaction times also coincided with decreased pre-stimulus activity in frontoparietal attentional cortices, such as the anterior cingulate, inferior frontal gyrus, and superior frontal gyrus, in comparison to faster reactions. These areas have previously been implicated in various aspects of attentional control, including conflict detection, reorientation of attention, and target detection (Carter et al. 2000; Corbetta and Shulman 2002; Kerns et al. 2004). As such, our results suggest that the use of attentional processes is reduced prior to slower reactions compared to faster reactions to stimuli.

Our results suggest that modulatory activity in both DMN and frontoparietal attentional regions plays an important role in not only attending to a stimulus but also responding on time to a stimulus, which is in accordance with a previous study by Weissman et al. (Weissman et al. 2006). Similarly to that study, in our group of younger adults, we found activity in DMN regions, such as the posterior cingulate and middle temporal gyrus, varied with reaction times. However, in comparison to the young adults in our study, the mechanisms underlying RT variability appeared to change in older adults. Young adults displayed BOLD activity that was significantly more positively modulated by reaction time, compared to older adults, in mainly DMN areas, such as the medial frontal gyrus, parahippocampal gyrus, and posterior cingulate. This finding is compatible with previous research that has found reduced magnitude of task-induced deactivations in the DMN in older adults compared to young adults (Grady et al. 2006; Lustig et al. 2003). Furthermore, older adults displayed BOLD activity that was significantly more positively modulated by reaction time, compared to young adults, in frontal areas related to attention, such as the anterior cingulate and inferior frontal gyrus. Our finding regarding greater and bilateral frontal activity in older adults during an attentional task is consistent with previous reports that have shown age-related increases in bilateral prefrontal activity across a variety of cognitive processes, such as memory retrieval, working memory, visual perception, and response inhibition (Cabeza 2002; Grady, Bernstein, Beig, and Siegenthaler 2002; Grady et al. 1994; Nielson, Langenecker, and Garavan 2002; Reuter-Lorenz et al. 2006).

The present study has a number of limitations. The use of vocal responses rather than button-press responses may have amplified motion artifacts. However, as we described in our methods, we used standard procedures to minimize the impact of motion on our data. A second potential limitation was the lack of statistically significant behavioral differences between the younger and older participants. This could be counter-intuitive as older adults may be expected to have slower reaction times than their younger counterparts. However, the younger adults appeared to have performed qualitatively faster, as seen in Table 1. The lack of significant difference

may be due to the relatively small sample sizes of both age groups, which may have inflated the variability of reaction times in each group, or the use of a trial-by-trial version of the Stroop test, which has been shown to reduce age effects on performance compared to blocked versions of the Stroop test (Ludwig, Borella, Tettamanti, and de Ribaupierre 2010). However, given the lack of consensus in the current literature regarding the Stroop task and aging as previously mentioned, our results are not out of line with previous studies.

Future studies are required to investigate causes behind age-related differences in RT-modulated neural activity. The recruitment of a greater number of frontal structures in older participants while they were engaged in the attentional task may be compensatory in nature, as prior research has shown that greater activity in older adults is associated with enhanced cognitive performance (Cabeza, Anderson, Locantore, and McIntosh 2002; Davis, Kragel, Madden, and Cabeza 2012; Reuter-Lorenz et al. 2006). Other work, however, has suggested that increased brain activity in older adults may be due to dedifferentiation (Grady 2008). The dedifferentiation hypothesis posits that activity in brain structures lose their specialization for specific functions over time. This view is supported by earlier evidence that patterns of brain activity across different tasks become less specialized, and thus more similar, in older adults (Carp, Park, Polk, and Park 2011; Dennis and Cabeza 2011). These neural mechanisms employed by older adults may be attributed to the reduced capacity of older adults to automatize task performance (Maquestiaux, Didierjean, Ruthruff, Chauvel, and Hartley 2013). At the present time, it is difficult to conclude whether the increased activity in older adults observed here are due to compensation or dedifferentiation, given that the previously mentioned literature has been focused on comparing high-performing and low-performing older adults against young adults, while the current study investigated age differences on the functional correlates of intra-individual RT variability. Regardless of these neural changes, the older group performed the task as effectively as the younger group. They also scored well on all behavioral measures, which suggests the presence of functional plasticity throughout the lifespan may contribute to healthy cognitive aging.

In conclusion, our findings provide new insights in the neural mechanisms underlying intra-individual reaction time variability throughout healthy aging. Our results show that activity in frontoparietal attentional regions and DMN areas varies proportionally with response time in a goal-directed task in both young and older adults. Our most critical finding shows that older adults exhibit greater reaction time-modulated activity in more frontal regions compared to younger adults. The increased activity demonstrated by older adults may reflect age-related mechanisms of compensation or dedifferentiation. Our findings suggest that while the functional correlates of intra-individual reaction time variability change

with age, the basic task-related mechanisms within frontoparietal attentional and default mode network regions remain stable throughout healthy aging.

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Conflict of interest Angela Tam, Angela C. Luedke, Jeremy J. Walsh, Juan Fernandez-Ruiz, and Angeles Garcia declare that they have no conflicts of interest.

Informed Consent All procedures followed were in accordance with the ethical standards of the responsible committee on human experimentation (institutional and national) and with the Helsinki Declaration of 1975, and the applicable revisions at the time of the investigation. Informed consent was obtained from all patients for being included in the study.

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