

Both left and right posterior parietal activations contribute to compensatory processes in normal aging

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ABSTRACT

Older adults often exhibit greater brain activation in prefrontal cortex compared to younger adults, and there is some evidence that this increased activation compensates for age-related neural degradation that would otherwise adversely affect cognitive performance. Less is known about aging and compensatory recruitment in the parietal cortex. In this event-related functional magnetic resonance imaging study, we presented healthy young and old participants with two Stroop-like tasks (number magnitude and physical size). In young, the number magnitude task activated right parietal cortex and the physical size task activated left parietal cortex. In older adults, we observed contralateral parietal recruitment that depended on the task: in the number magnitude task older participants recruited left posterior parietal cortex (in addition to the right parietal activity observed in young) while in the physical size task they recruited right (in addition to left) posterior parietal cortex. In both cases, the additional parietal activity was associated with better performance suggesting that it played a compensatory role. Older adults also recruited left prefrontal cortex during both tasks and this common activation was also associated with better performance. The results provide evidence for task-specific compensatory recruitment in parietal cortex as well as task-independent compensatory recruitment in prefrontal cortex in normal aging.

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1. Introduction

Numerous neuroimaging studies have reported that older participants exhibit greater activity in prefrontal cortex (PFC) than young adults across a range of tasks, with the most common pattern being greater bilateral activity when more unilateral activity is observed in young adults (Cabeza, 2002; Cabeza, Anderson, Locantore, & McIntosh, 2002; Cabeza et al., 2004; Davis, Kragel, Madden, & Cabeza, 2011; de Chastelaine, Wang, Minton, Muftuler, & Rugg, 2011; Reuter-Lorenz et al., 2000; Schneider-Garces et al., 2010). This additional prefrontal recruitment is so common across such a wide range of tasks that some authors have suggested that it is a general characteristic of age-related neural change (Cabeza et al., 2004; Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008; Spreng, Wojtowicz, & Grady, 2010).

This pattern of additional age-related PFC recruitment is often interpreted as being compensatory and is hypothesized to improve or maintain performance in the face of age-related neurodegeneration (Park & Reuter-Lorenz, 2009). Moreover, increased PFC activity with age frequently occurs in the context of decreased activation in posterior sites, including medial temporal lobe (Cabeza et al., 2004; Gutchess et al., 2005; Park et al., 2003), and ventral visual cortex (Cabeza et al., 2004; Davis et al., 2008; Goh, Suzuki, & Park, 2010), consistent with the idea that PFC overrecruitment may compensate for dysfunction in other brain areas (Park & Reuter-Lorenz, 2009).

Posterior parietal cortices (PPC), including superior and inferior parietal lobules, have also been found to exhibit increased activity in older compared to younger adults. These regions have previously been associated with selective attention, memory retrieval, mental calculation, and cognitive control (Corbetta & Shulman, 2002; Dehaene, Molko, Cohen, & Wilson, 2004; Derrfuss, Brass, Neumann, & von Cramon, 2005; Roberts & Hall, 2008; Wager et al., 2005). Age-related activation increases in these areas have been reported during demanding tasks, including task switching (DiGirolamo et al., 2001; Jimura & Braver, 2010), control of response inhibition (Nielson, Langenecker, & Garavan, 2002; Nielson et al., 2004; Vallesi, McIntosh, & Stuss, 2011; Zhu, Zacks, & Slade, 2010), motor

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Table 1
Participant characteristics, demographics, and neuropsychological assessment (means and standard deviations).

	Young		Older		p-value
	Mean	SD	Mean	SD	
Age	25.53	3.48	66.07	4.15	0.00**
Year of education	16.67	1.99	16.47	2.03	0.79
Mini-Mental State Exam	29.20	1.42	28.60	0.99	0.19
Shipley Vocabulary Task	34.87	3.11	36.36	2.27	0.16
Pattern Matching	43.13	5.63	30.20	7.85	0.00**
Dot Matching	17.00	2.93	10.27	2.81	0.00**
Letter-Number Sequencing	15.27	1.94	11.47	3.62	0.00**
WAIS-R Digit-Symbol	79.47	8.76	58.53	9.43	0.00**
WAIS-Information	24.20	2.62	24.40	3.44	0.86
WMS-III Forward Spatial Span	10.20	1.61	7.47	1.51	0.00**
WMS-III Backward Spatial Span	9.53	1.60	8.27	1.44	0.03*

* $p < 0.05$.

** $p < 0.01$.

control (Heuninckx, Wenderoth, Debaere, Peeters, & Swinnen, 2005; Heuninckx, Wenderoth, & Swinnen, 2008) and resolution of interference (Langenecker, Nielson, & Rao, 2004; Prakash et al., 2009; Zysset, Schroeter, Neumann, & Yves von Cramon, 2007).

In this study we investigate two questions: (1) does additional recruitment of parietal cortex serve a compensatory function in older adults and (2) are the additional prefrontal and parietal areas that are activated in older adults recruited for specific tasks or are they shared across tasks? To investigate these questions, we used event-related functional magnetic resonance imaging (fMRI) to examine neural activity in young and older adults while they performed two Stroop-like tasks that are known to produce unilateral activity on opposite sides of parietal cortex in young adults (Kaufmann et al., 2005; Liu, Wang, Corbly, Zhang, & Joseph, 2006; Tang, Critchley, Glaser, Dolan, & Butterworth, 2006). Specifically, we used a modified version of the physical-numerical interference paradigm (Besner & Coltheart, 1979) that allowed us to evaluate conflict judgments regarding physical size and numerical magnitude in two tasks using identical stimuli. Previous fMRI studies found predominantly left-lateralized fronto-parietal activation in young adults for the physical size task and primarily right-lateralized fronto-parietal activation for the numerical magnitude task (Kaufmann et al., 2005; Liu et al., 2006; Tang et al., 2006).

We hypothesized that elderly participants would deploy additional left parietal regions on the numerical judgment task which is right-lateralized in young, and similarly, expected that the same elderly subjects would deploy more right-parietal regions on the physical size judgment task that is left-lateralized in young. We hoped to demonstrate that older adults could flexibly activate additional left or right parietal cortex, depending on task demands, and that the level of additional activation in each hemisphere would be related to better task performance for the particular task being performed. Such a result would provide strong evidence for compensatory recruitment of both left and right parietal lobe deployed selectively by older adults according to task demands. In addition, we also examined the role of additional frontal lobe recruitment on these two tasks, as enhanced frontal recruitment with age has been widely reported across many studies.

2. Methods

2.1. Participants

A total of 15 young adults (mean age 25.5 years, range 21 to 32 years; 9 females) and 18 healthy community-dwelling older adults (mean age 66.1 years, range 61 to 73 years; 9 females) participated in the study. The study was approved by the University of Illinois at Urbana-Champaign Institutional Review Board and all participants gave informed consent prior to their participation. We discarded the data

from three older participants because of excess motion (two participants) and image distortion due to improper headcoil placement (one participant). All participants were right-handed native English speakers with normal or corrected-to-normal vision and had no prior history of psychiatric or neurological disorders. Young and older participants had a minimum score of 26 on the Mini-Mental State Exam (MMSE; (Folstein, Folstein, & McHugh, 1975), with mean scores of 29.2 for young and 28.6 for old. Young and older participants had equivalent levels of education and verbal ability as measured on the Shipley Vocabulary task (Shipley, 1986), as shown in Table 1. In addition, older adults exhibited lower scores on the WAIS-R Digit-Symbol coding (Wechsler, 1997a), Pattern Matching and Dot Matching, which measured speed of processing, as well as Letter-Number Sequencing, and Forward and Backward Spatial Span (Wechsler Memory Scale-III, Wechsler, 1997b), which measured working memory. This pattern of stable crystallized ability (Shipley Vocabulary) with age and lower fluid abilities (speed and working memory) is typical of most cognitive aging samples in the literatures that focus on normal aging (Park et al., 2002). Group characteristics and results are reported in Table 1.

2.2. Experimental material and design

Prior to entering the scanner, all participants underwent a short training session and practiced modified versions of the physical-numerical interference paradigm used by Besner and Coltheart (1979). Two types of magnitude judgments were included in this modified paradigm: a physical size task and a numerical magnitude task (see Fig. 1). In the physical size task, participants were presented with a pair of digits and were required to judge which digit was physically larger while ignoring the numerical magnitude of the digits. On the other hand, in the numerical magnitude task, participants were also presented with a pair of digits and were asked to indicate which was numerically larger while ignoring their physical size. In both tasks, individual digits between 1 and 9, excluding 5 (Tzelgov, Meyer, & Henik, 1992), were used to create the digit pairs, and digit pairs were presented in Arial font with two different font sizes (55 and 73) to manipulate the physical size of the items.

For each task, we created digit pairs with three different levels of congruity. In congruent trials, the digit that was larger in magnitude was also larger in physical size. In incongruent trials, the digit that was larger in magnitude was smaller in physical size. Finally, in neutral trials the two digits were matched on the task-irrelevant dimension: for the physical size task, neutral pairs involved the same numerical value (e.g., 6 6); for the numerical magnitude task, neutral pairs had the same physical size (e.g., 2 6).

The functional MRI session was divided into four runs with two runs for each task. The order of the four runs was counter-balanced across participants, and stimuli within each run were presented randomly to control for order and fatigue effects. Each run consisted of 48 experimental trials, yielding 192 trials in total. The 48 trials within each run consisted of 16 congruent, 16 incongruent and 16 neutral trials, with each trial consisting of a 500 ms fixation-cross and 500 ms blank screen followed by a 1000 ms presentation of the stimulus (see Fig. 1). Trials were jittered and separated by inter-trial intervals (ITI) of 2, 4 or 6 s with a mean separation of 4 s (Dale, 1999). A resting period of 21 s with a fixation-cross was presented at the beginning and end of each run, yielding a run lasting 330 s in total.

Stimuli were presented via E-prime (Psychology Software Tools, Pittsburgh, PA, USA) with a back-projection system. Participants viewed the stimuli using a mirror mounted on the headcoil and indicated their responses with a button press using the index and middle fingers of their right hand (Lumina response pad; Cedrus, San Pedro, CA, USA). Before each run, participants were orally and visually instructed to identify which digit in each pair was numerically (in the numerical magnitude task) or physically (in the physical size task) larger, and to respond as quickly and accurately as possible.

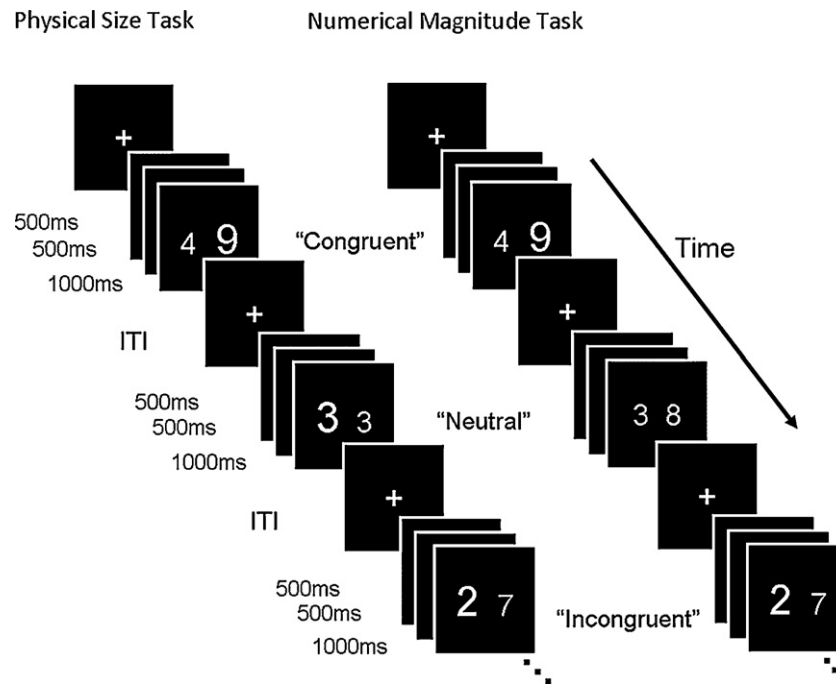


Fig. 1. Experimental procedures showing sample stimuli for the congruent, neutral, and incongruent conditions in both tasks. Each trial consisted of a 500 ms fixation-cross and 500 ms blank screen followed by a 1000 ms presentation of the stimulus. Inter-trial-intervals (ITI) varied between 2, 4, and 6 s. The physical size task and numerical magnitude task each occurred twice in counter-balanced order across participants.

2.3. Imaging acquisition and preprocessing

All fMRI sessions were conducted on a 3.0T MRI scanner (Allegra, Siemens, Germany) at the University of Illinois at Urbana-Champaign. For the experimental task, 165 functional scans were acquired in each run using a single-shot T2*-weighted gradient-echo echo-planar image (EPI) sequence with TR/TE/FA = 2000 ms/60 ms/90°. Thirty-six contiguous axial slices were acquired with a slice thickness of 3 mm, 64 × 64 acquisition matrix, and 3.3 mm × 3.3 mm in-plane resolution. Co-planar structural T2 images were acquired to co-register the functional images to 3D-MPRAGE T1 structural image also acquired for each participant.

All preprocessing and general linear model (GLM) estimation was carried out using SPM2 software (Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK) implemented in MATLAB version 7.0 (The MathWorks, Natick, MA, USA). After discarding the first five volumes of each run, the functional images were corrected for slice acquisition time and for participant motion, spatially normalized to the Montreal Neurological Institute (MNI) template and then spatially smoothed using an 8-mm full-width-at-half-maximum (FWHM) Gaussian kernel. Low frequency noise was also removed with a high-pass filter.

2.4. fMRI data analysis

The physical size and numerical magnitude tasks were modeled separately. Within each task, event-related BOLD responses for the congruent and incongruent conditions were modeled for each participant by convolving a vector of the onset times of the stimuli with the canonical hemodynamic response function (HRF) within the context of the GLM implemented in SPM2. Only correct trials were included in the models.

To identify brain regions involved in interference resolution, we contrasted the incongruent and congruent conditions for the physical size and numerical magnitude tasks separately in each participant. The resulting contrast maps were then subjected to a second-level random effects analysis to identify brain regions that were significantly activated by the contrast across participants or that were significantly more activated in one age group compared with the other. Significant regions of activation were identified using an uncorrected threshold of $p < 0.001$ and a minimum cluster size of 10 contiguous voxels.

3. Results

3.1. Behavioral results

Table 2 presents the behavioral results. We performed a $2 \times 2 \times 3$ analysis of variance (ANOVA) on the accuracy data with age (young adults, older adults) as a between-subject factor and

task (physical size, numerical magnitude) and level of congruity (congruent, incongruent, neutral) as within-subject factors. The task had a significant effect on accuracy [$F(1,28) = 6.28$, $p < 0.05$, $\eta^2 = 0.18$], with lower accuracy for the numerical magnitude task compared to the physical size task. Congruity also significantly affected accuracy [$F(2,27) = 22.74$, $p < 0.001$, $\eta^2 = 0.63$], with lower accuracy for the incongruent condition compared to the congruent [$t(118) = -5.99$, $p < 0.01$] and neutral [$t(118) = -5.21$, $p < 0.01$] conditions. There were no significant differences in accuracy between the neutral and congruent conditions [$t(118) = 0.32$, $p = 0.38$]. The interaction between task and congruity was also significant [$F(2,27) = 4.92$, $p < 0.05$, $\eta^2 = 0.27$] with a greater congruity effect for the numerical magnitude task than the physical size task. There was no significant effect of age on accuracy [$F(1,28) = 2.25$, $p = 0.15$], and age did not interact with task [$F(1,28) = 0.04$, $p = 0.84$] or congruity [$F(2,27) = 0.42$, $p = 0.66$]. In sum, accuracy was greater on the physical size task and in the congruent condition, but similar accuracy was obtained for young and older adults.

Error trials were removed from all subsequent analyses of reaction time. The same age × task × congruity ANOVA on the RT data yielded a significant effect of age [$F(1,28) = 46.63$, $p < 0.01$, $\eta^2 = 0.63$], of task [$F(1,28) = 62.17$, $p < 0.01$, $\eta^2 = 0.69$] and of congruity [$F(2,27) = 86.18$, $p < 0.01$, $\eta^2 = 0.87$]: older adults were slower, responses on the numerical magnitude task were slower, and the incongruent condition was slower. Post hoc tests indicated that responses were slower in the incongruent condition compared to the congruent [$t(118) = 4.75$, $p < 0.01$] and neutral [$t(118) = 3.55$, $p < 0.01$] conditions. There were no significant differences in RT between the congruent and neutral conditions [$t(118) = 1.30$, $p = 0.10$]. There was also a reliable task × congruity interaction [$F(2,27) = 11.40$, $p < 0.01$, $\eta^2 = 0.46$], with a larger congruity effect in the numerical magnitude task than in the physical size task. Once again, age did not significantly interact with task [$F(1,28) = 0.77$, $p = 0.03$] or with congruity [$F(2,27) = 2.18$, $p = 0.14$].

Overall, older adults generally responded slower than young adults but with comparable accuracy. Both accuracy and RTs were worse on incongruent trials compared with congruent and neutral

Table 2
Response times (ms), mean accuracy and standard deviations for young and older adults in the physical size task and numerical magnitude task as a function of congruity.

	Young		Older	
	RTs (ms)	Accuracy	RTs (ms)	Accuracy
Physical size task				
Congruent	449.6 (43.0)	0.99 (0.0)	550.5 (75.8)	0.99 (0.0)
Neutral	459.9 (63.1)	0.98 (0.1)	564.1 (91.5)	0.99 (0.0)
Incongruent	506.7 (59.5)	0.95 (0.1)	642.1 (101.3)	0.97 (0.0)
Numerical magnitude task				
Congruent	503.4 (54.6)	0.98 (0.0)	636.4 (84.2)	0.99 (0.0)
Neutral	545.5 (89.8)	0.98 (0.1)	667.7 (100.1)	0.99 (0.0)
Incongruent	608.4 (76.5)	0.93 (0.1)	759.8 (83.7)	0.94 (0.1)

Note: Numbers in parentheses denote standard deviations.

trials and on the numerical magnitude task compared with the physical size task.

3.2. fMRI results

3.2.1. Incongruent vs. congruent contrast

An initial direct comparison of the incongruent vs. congruent condition (collapsed across age and tasks) yielded significant activations in several frontal and parietal regions that have been previously reported in other studies using similar interference paradigms (Kaufmann et al., 2005; Wood, Ischebeck, Koppelstaetter, Gotwald, & Kaufmann, 2009). Table 3 reports brain regions that were activated by the incongruent vs. congruent contrast in each task across the two age groups. Both tasks activated left and right inferior and middle frontal gyrus, anterior cingulate cortex, bilateral inferior parietal cortex, right precuneus, and bilateral cerebellum (see Fig. 2), which have been proposed to be involved in interference resolution (Nee, Wager, & Jonides, 2007; Roberts & Hall, 2008). Because we are primarily interested in age and task differences, we now focus on analyses that included these as variables.

3.2.2. Task-specific age-related neural overrecruitment

We next examined how age affected the neural substrates of interference resolution for each task. Whereas both age groups showed significant frontal and parietal activity, older adults recruited a larger and more distributed network compared to young adults, especially in posterior parietal cortices. Fig. 3 shows the results of the incongruent vs. congruent contrast in posterior parietal cortex for each task within each age group (Fig. 3, left) as well as parietal areas that were significantly more activated in the older participants compared to the young (Fig. 3, middle and right). Results from the physical size task are in the top panel (Fig. 3a) and results from the numerical magnitude task are in the bottom panel (Fig. 3b).

The young participants exhibited strongly left-lateralized parietal activity during the physical size task and strongly right-lateralized parietal activity during the numerical magnitude task (Fig. 3, left). The older participants also activated these regions, but in addition they engaged unique contralateral parietal regions for each task: on the physical size task, older adults showed additional activation compared to young in the right superior and inferior parietal lobules (MNI coordinate of peak: 36, −44, 54). On the numerical magnitude task, they showed additional activation in the left superior and inferior parietal lobules (MNI coordinate of peak: −30, −62, 42).

A direct comparison between the two age groups clearly demonstrates the task-specific age-related contralateral recruitment in posterior parietal cortex (Fig. 3, middle and Table 4). Older adults activated parietal cortex in the non-preferred hemisphere significantly more than young adults did and did so in a selective manner. That is, the older adults exhibited additional

activity in left parietal cortex for the numerical magnitude task, and in right parietal cortex for the physical size task. In addition, a direct contrast of age on each task showed that for the physical size task, old activated more than young in bilateral precentral gyri, right superior frontal, and left inferior frontal regions, but there was no significant difference in frontal activity between the age groups for the numerical magnitude task (Table 4).

3.2.3. Age-related neural overrecruitment across tasks

The location of the additional parietal activity in the older participants depended on the task. For the physical size task, older participants engaged additional right posterior parietal cortex compared with the young, but for the numerical magnitude task they engaged additional left posterior parietal cortex. Moreover, there were also some specific frontal regions that showed domain-specific overrecruitment in older adults. We next examined whether there were regions in prefrontal and parietal areas that exhibited overrecruitment by the older participants across both tasks.

To identify such common brain regions, we performed a whole brain conjunction analysis across both tasks. We first identified regions that were significantly more active for the incongruent vs. congruent contrast in older versus young adults in the physical size and numerical magnitude tasks separately. We then intersected the two maps to identify regions that were significantly more active in the older subjects on both tasks. For this conjunction analysis, we used a threshold of $p < 0.005$ with an extent threshold of 10 contiguous voxels.

Fig. 4 and Table 5 show the results. Older adults showed greater activity in bilateral PFC, supplementary motor area (SMA), left precentral gyrus, left superior temporal gyrus, and bilateral cerebellum, indicating a pattern of task-invariant age-related overrecruitment in these regions during interference resolution. In contrast, we did not find any brain regions that exhibited greater activity in young adults compared to older adults. Importantly, we also did not find age-related differences in parietal regions across the two tasks, suggesting that additional parietal recruitment in older adults is sensitive to the specific task domain.

3.2.4. Age-related differences in laterality

We next looked for evidence of age-related laterality differences in prefrontal and parietal cortex, as well as in anterior cingulate cortex (a control region where laterality differences were not expected between young and old). Systematic assessments of the laterality of activation were performed over three anatomically defined regions-of-interest (ROIs): (1) bilateral PFC (including superior, middle and inferior frontal gyrus), (2) bilateral PPC (including superior and inferior parietal lobules), and (3) anterior cingulate

Table 3

Peak locations of regions associated with interference resolution (incongruent vs. congruent) during the physical size task and numerical magnitude task across age groups (≥ 10 contiguous voxels with $p < 0.001$, uncorrected).

Brain regions		L/R	BA	x	y	z	t-value
Physical size task							
Frontal cortex	Inferior frontal	R	44/47	44	24	2	6.88
		L	44	−54	12	18	3.57
	Middle frontal	R	9/10	32	44	10	5.28
		L	9/46	−38	8	34	4.81
	ACC	B	32	10	20	42	5.27
	SMA	B	6/24	14	8	42	4.62
	Insula	L	13	−30	10	12	4.03
	Precentral gyrus	L	4/6	−48	6	44	3.84
	Inferior parietal	L	40	−32	−50	48	5.65
		R	40	38	−48	46	4.19
Parietal cortex	Supramarginal	R	2	60	−32	50	4.53
	Precuneus	R	7	12	−66	64	4.26
	Superior parietal	R	7	34	−56	60	4.06
		L	–	−8	−46	−18	4.89
Cerebellum		R	–	16	−48	−44	4.89
Superior temporal		R	41	46	−28	6	4.77
Middle/inferior temporal		L	22	−52	−50	14	3.81
Thalamus		L	–	−6	−22	6	3.79
Numerical magnitude task							
Frontal cortex	Inferior frontal	R	45	52	20	14	5.18
		L	44/45	−36	28	8	4.84
	Superior frontal	R	9/47	28	58	32	4.33
	ACC	B	6	8	22	20	4.09
	Middle frontal	L	10/46	−32	50	36	4.04
		R	10/46	40	56	8	3.83
Parietal cortex	Precuneus	R	7	16	−68	48	5.84*
	Inferior parietal	R	7	16	−68	50	5.71*
		L	40	−48	−38	44	4.06
	Superior parietal	L	7	−12	−70	42	4.47
	Supramarginal	R	40	62	−36	34	4.31*
		L	–	−30	−58	−36	5.68
Cerebellum		R	–	36	−50	−32	5.27
Superior occipital		L	7	−24	−72	32	5.12
Thalamus		L	–	−14	−24	10	4.37

L, left; R, right; B, bilateral hemispheres; k, cluster size in voxel; BA, Brodmann's area; ACC, anterior cingulate cortex; SMA, supplementary motor area.

* Peaks in the same cluster.

Table 4

Peak locations of regions showing age-related differences in brain activity during interference resolution (incongruent vs. congruent) specific to the physical size task and numerical magnitude task (≥ 10 contiguous voxels with $p < 0.001$, uncorrected).

Brain regions		L/R	BA	x	y	z	t-value
Older > Young: Physical size task							
Frontal cortex	Precentral	L	6	−28	−18	72	4.38
		R	3	32	−32	74	3.60
	Superior frontal	R	6	38	−6	66	4.01
	SMA	B	6	6	−2	70	3.97
	ACC	B	32	−4	30	−10	3.70
	Inferior frontal	L	47	−24	12	−26	3.60
	Middle frontal	R	10	34	62	8	3.54
	Inferior parietal	R	40	36	−44	54	3.98
		L	–	−22	−44	−24	5.48
	Cerebellum	R	–	20	−68	−20	3.77
Superior temporal		R	41	46	−28	14	4.68
Young > Older: Physical size task							
No significant activation							
Older > Young: Numerical magnitude task							
Parietal cortex	Inferior parietal	L	7	−30	−62	42	3.96
		R	40	38	−50	44	3.66
	Angular	L	40	−32	−54	34	3.91
	Superior parietal	L	7	−12	−72	40	3.60
		R	22	58	−32	0	3.48
Middle temporal		R	22	58	−32	0	3.48
Young > Older: Numerical magnitude task							
No significant activation							

L, left; R, right; B, bilateral hemispheres; BA, Brodmann's area; ACC, anterior cingulate cortex; SMA, supplementary motor area.

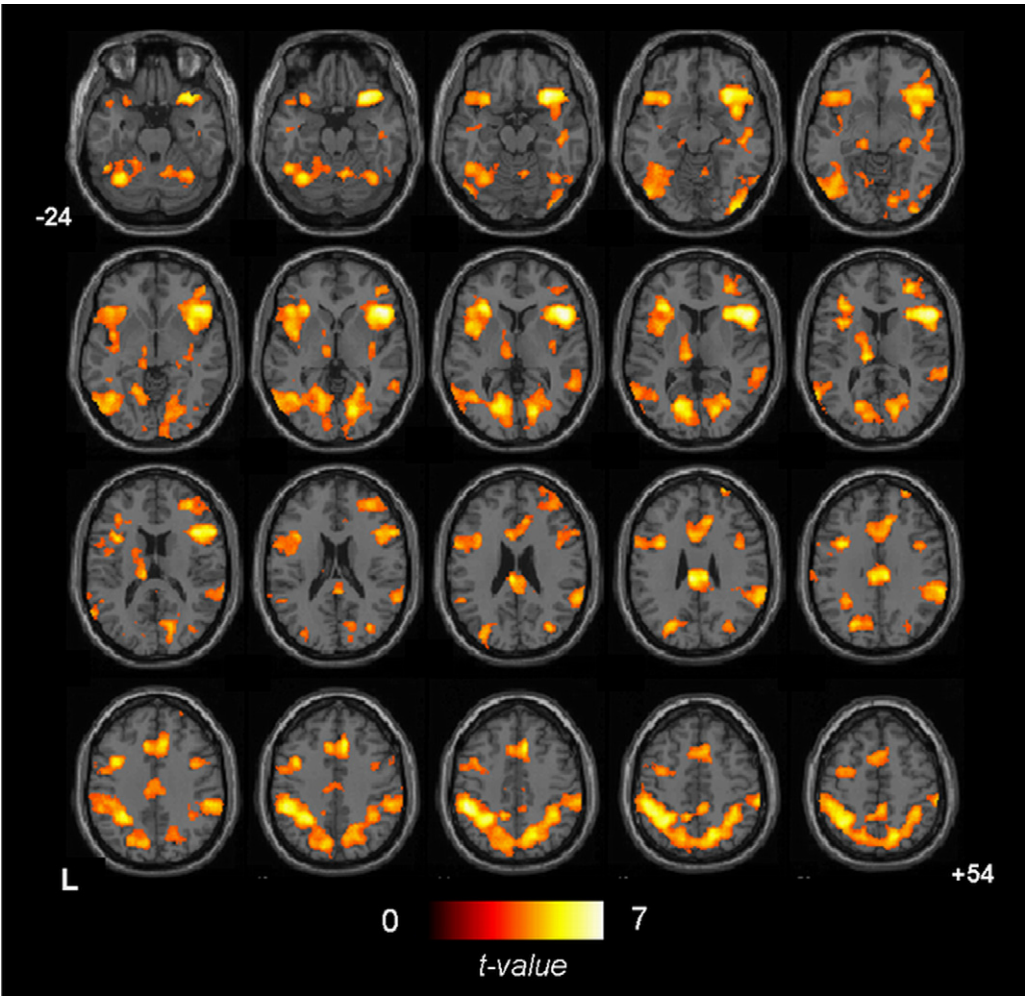


Fig. 2. Effect of congruity. Group statistical brain map (axial view) of the incongruent vs. congruent contrast for all participants, collapsed across tasks (≥ 10 contiguous voxels with $p < 0.001$, uncorrected). L = the left hemisphere.

cortex (ACC). Laterality indices were based on the standard formula (Everts et al., 2009):

$$\text{Laterality} = \left[\frac{(\sum \text{voxel}_{\text{left}} - \sum \text{voxel}_{\text{right}})}{(\sum \text{voxel}_{\text{left}} + \sum \text{voxel}_{\text{right}})} \right]$$

This formula results in positive values for predominantly left-lateralized activity (laterality > 0) and negative values for predominantly right-lateralized activity (laterality < 0).

To ensure the findings of age-related bilateral recruitment in PFC and PPC were not due to the selected significance threshold

(Cabeza, 2002), we computed laterality indices based on a variety of different activation thresholds and then computed a weighted average of the laterality indices, giving more weight to indices that were computed using higher thresholds (Wilke & Schmithorst, 2006). This approach has been used in previous work to assess the hemispheric asymmetry of verbal and visuospatial functions across the lifespan (Everts et al., 2009).

Fig. 5 shows the results. For the physical size task (Fig. 5a), young adults exhibited strongly left-lateralized activation in PPC (laterality: mean = 0.32, S.D. = 0.11) whereas older adults' activation was not strongly lateralized (laterality: mean = 0.05, S.D. = 0.08).

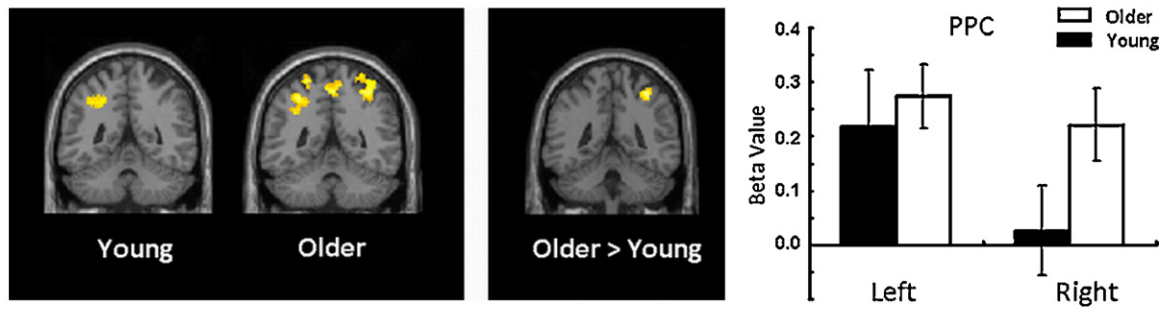
Table 5
Peak locations of regions showing age-related overrecruitment during interference resolution (incongruent vs. congruent) across both the physical size and numerical magnitude tasks (≥ 10 contiguous voxels with $p < 0.005$, uncorrected).

Brain regions	L/R	BA	x	y	z	t-value
Older > Young: Physical size task \cap Numerical magnitude task						
Precentral	L	6	-52	-6	52	3.12
Inferior/middle frontal	L	46	-36	52	22	3.02
Middle frontal	R	10/46	34	60	22	2.74
SMA	B	6	-10	-10	62	3.04
Superior temporal	L	22	-60	-36	12	2.97
Cerebellum	L	-	-20	-34	-26	3.21
	R	-	12	-54	-22	3.05
Young > Older: Physical size task \cap Numerical magnitude task						
No significant activation						

L, left; R, right; B, bilateral hemispheres; BA, Brodmann's area; SMA, supplementary motor area.

Physical Size Task

a



Numerical Magnitude Task

b



Fig. 3. Task-specific age-related neural overrecruitment in the posterior parietal cortex (PPC) during the (a) physical size task, and (b) numerical magnitude task. The leftmost panel presents coronal slices showing the incongruent vs. congruent contrast for each age group. The middle panel shows the parietal areas that were significantly more activated in the older participants compared to the young. The rightmost panel shows regions-of-interest analyses for both age groups in the parietal regions that were recruited selectively by the older subjects, as well as in the homologous region of the preferred hemisphere that was activated by both. Error bars denote S.E.

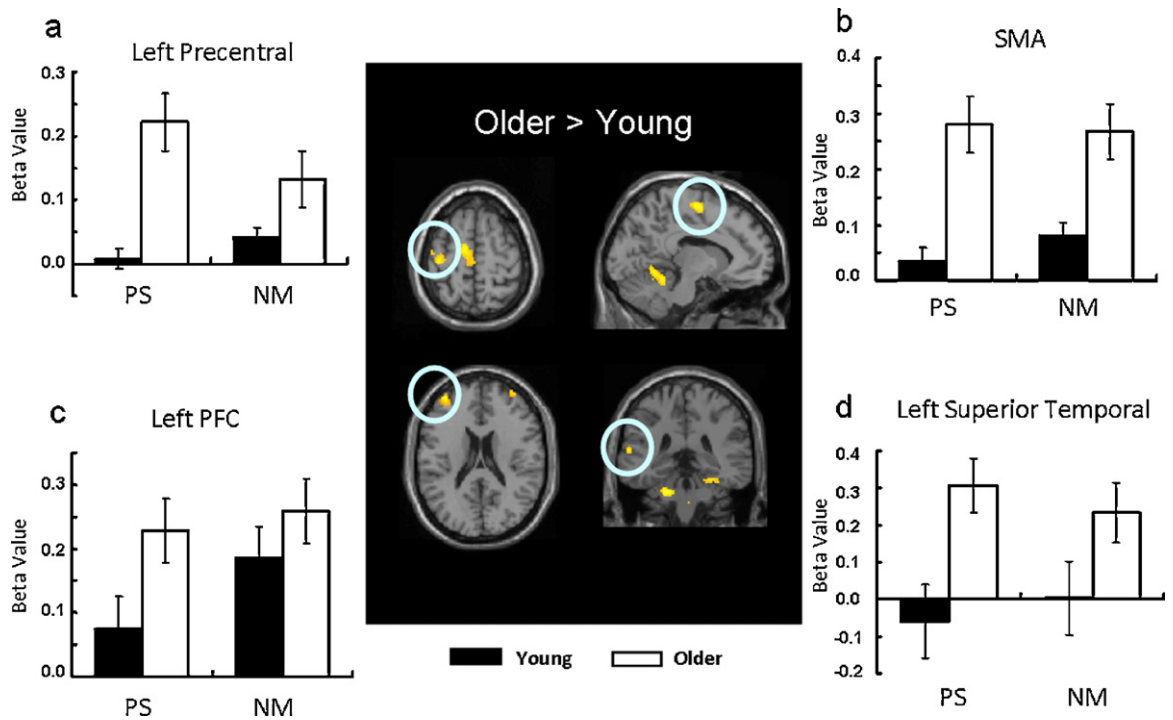


Fig. 4. Age-related neural overrecruitment across tasks. Conjunction analysis showing regions exhibiting greater activity (incongruent vs. congruent) in the old compared to the young across both the physical size and numerical magnitude tasks (≥ 10 contiguous voxels with $p < 0.005$, uncorrected in both tasks). Average parameter estimates during the physical size (PS) and numerical magnitude (NM) tasks are shown for (a) left precentral gyrus, (b) supplementary motor area (SMA), (c) left prefrontal cortex (PFC), and (d) left superior temporal gyrus. Error bars denote S.E.

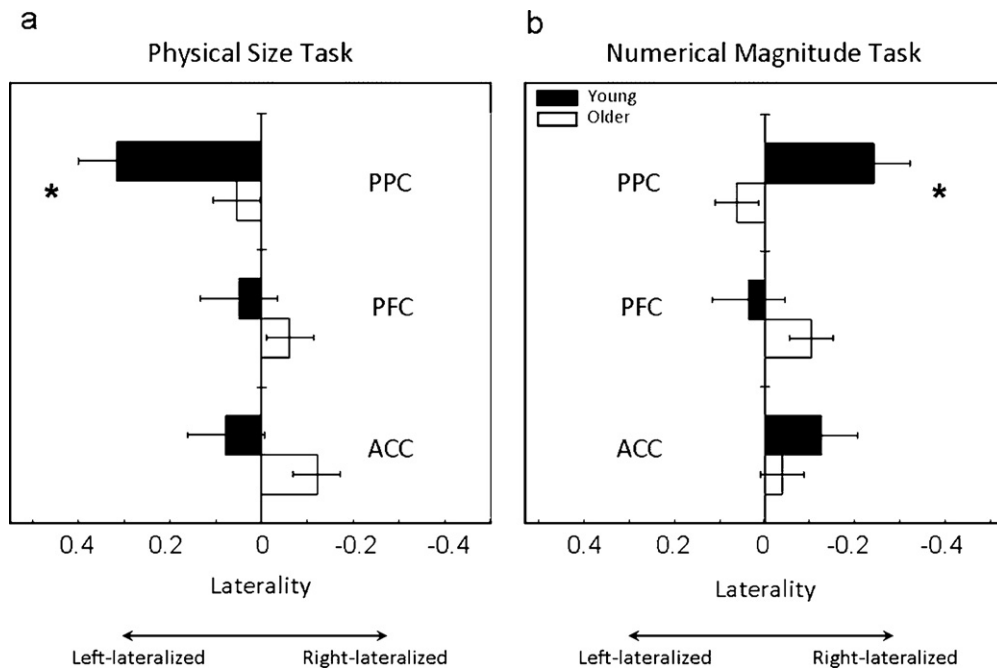


Fig. 5. Age-related differences in laterality. The threshold-weighted mean values indicate laterality of functional activation over posterior parietal cortex (PPC), prefrontal cortex (PFC), and anterior cingulate cortex (ACC) in young and older adults for (a) physical size task and (b) numerical magnitude task. Laterality are calculated according to the formula: $[(\Sigma \text{voxel}_{\text{left}} - \Sigma \text{voxel}_{\text{right}}) / (\Sigma \text{voxel}_{\text{left}} + \Sigma \text{voxel}_{\text{right}})]$, with positive values for predominantly left-lateralized activation (laterality > 0) and negative values for primarily right-lateralized activation (laterality < 0). * $p < 0.05$.

The difference in lateralization between the young and older participants was significant [$t(28) = 2.30$, $p < 0.05$]. Similarly, for the numerical magnitude task (Fig. 5b), young adults exhibited right-lateralized activation in PPC (laterality: mean = -0.24 , S.D. = 0.06), whereas older adults did not (laterality: mean = 0.06 , S.D. = 0.17). This difference was also significant [$t(28) = 1.71$, $p < 0.05$]. These age-related lateralization differences were specific to PPC however. We found no significant difference in the laterality indices of young vs. older adults in PFC or ACC on either the physical size task [PFC: $t(28) = 0.80$, $p = 0.20$; ACC: $t(28) = 1.24$, $p = 0.11$] (Fig. 5a) or the numerical magnitude task [PFC: $t(28) = 1.08$, $p = 0.14$; ACC: $t(28) = 0.45$, $p = 0.33$] (Fig. 5b).

3.2.5. The effect of age-related neural overrecruitment on performance

Finally, we investigated whether older participants who exhibited more activity in the brain regions where we observed age-related neural overrecruitment also exhibited better performance. Such a finding would suggest that the additional activation is compensatory rather than harmful.

To control for individual differences in overall reaction time, we computed a proportional interference RT score for each participant using the following formula (Colcombe, Kramer, Erickson, & Scalf, 2005; Langenecker et al., 2004):

$$\text{Interference (\%)} = \left[\frac{(\text{RT}_{\text{Incongruent}} - \text{RT}_{\text{congruent}})}{\text{RT}_{\text{congruent}}} \right] \times 100$$

Larger positive interference percentages indicate greater interference and values around 0 indicate the absence of interference.

We then computed the correlation between these interference percentages and the older participants' activation in each of the regions where age-related neural overrecruitment was observed (the two domain-specific PPC regions in the middle of Fig. 3 and the seven regions in Table 5). Activation in each ROI was measured as the average percent signal change for the incongruent vs. congruent condition in all voxels in a 6 mm sphere surrounding the peak voxel.

Those average percent signal changes were then transformed into z-scores.

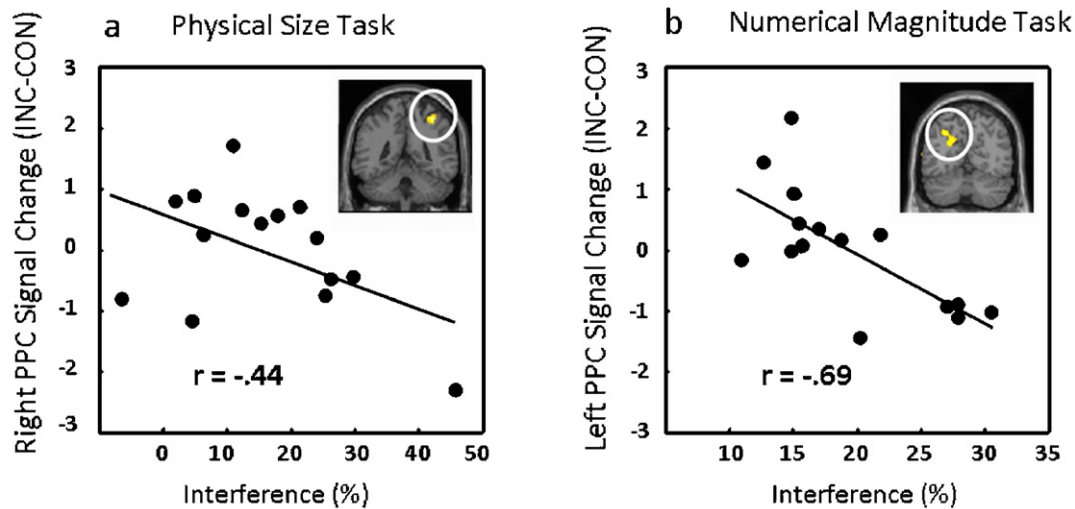
In older adults, the interference percentage was negatively correlated with activation of right PPC during the physical size task (Fig. 6a, $r = -0.44$, $p < 0.05$), indicating better performance (less interference) with greater neural recruitment. Similarly, the interference percentage was negatively correlated with activation of left PPC during the numerical magnitude task (Fig. 6b, $r = -0.69$, $p < 0.01$).

Activity in the left PFC region that was recruited by older adults across both tasks was also negatively correlated with the interference percentage in both tasks. Specifically, left inferior and middle frontal gyrus activity was negatively correlated with the interference percentage in the physical size task (Fig. 6c, $r = -0.49$, $p < 0.05$) and the numerical magnitude task (Fig. 6d, $r = -0.47$, $p < 0.05$). These results indicate an age-related compensatory process in left inferior frontal cortex. However, we did not find a significant negative correlation between the interference percentage and additional activity in any of the other areas from Table 5 that exhibited age-related neural overrecruitment.

3.2.6. Timecourse of compensatory activity

Finally, we examined the timecourse of compensatory activity in parietal and prefrontal cortex in order to investigate whether the compensatory activity begins at the same time as the activity observed in young subjects or if it is delayed. Average time courses for incongruent trials were extracted from the left PFC (Table 5), right PPC and left PPC (Table 4), averaging across trials and across voxels within each ROI. Fig. 7 shows the results. As can be seen, there was no evidence of a temporal delay in the compensatory activity. Both of the compensatory regions in the physical size task (the right PPC and left PFC) became active at the same time as the region used by young adults (the left PPC). Similarly in the numerical magnitude task, the compensatory regions (left PPC and left PFC) became active at the same time as the region used by young adults (right PPC). Our results thus suggest that

Task-Specific Posterior Parietal Compensation



Task-invariant Left Prefrontal Compensation

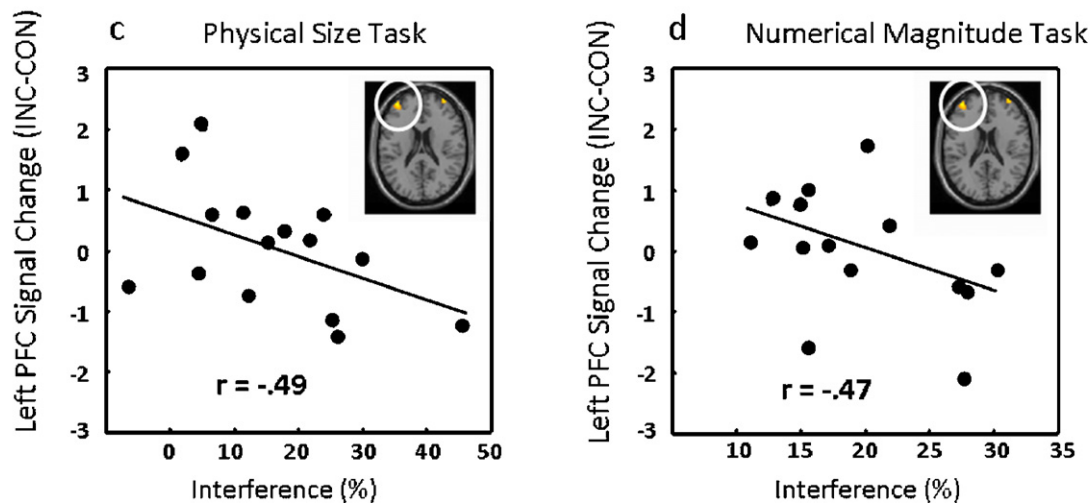


Fig. 6. The effect of age-related neural overrecruitment on performance in the older participants. Correlation between standardized percent signal changes during interference resolution (incongruent vs. congruent) and RT interference percentage (proportional interference score) for the physical size task (left) and numerical magnitude task (right) in each of the regions that showed age-related neural overrecruitment. Top-panel: Greater recruitment of right posterior parietal cortex (PPC) was associated with better performance in the physical size task (a) and greater recruitment of left PPC was associated with better performance in the numerical magnitude task (b). Bottom-panel: Greater recruitment of left prefrontal cortex was associated with better performance in both the physical size task (c) and the numerical magnitude task (d). Best-fitting regression lines (and r values) are shown.

the compensatory activity begins immediately rather than being delayed.

4. Discussion

In this study, we investigated age-related neural recruitment in parietal cortex. A number of previous studies have found that older adults recruit regions of frontal cortex that are contralateral to the regions activated by younger adults. We asked whether a similar phenomenon occurs in parietal cortex. We found that it does, and in a task-specific manner.

We used two numerical Stroop tasks that activate opposite sides of posterior parietal cortex (PPC) in young adults. In the number magnitude task, older adults recruited left PPC in addition to the right parietal activity that they shared with young adults. In the physical size task, older adults recruited right PPC in addition to

the left parietal activity that they shared with young adults. These results demonstrate task-specific age-related neural recruitment in PPC, as the hemisphere that was recruited depended on the judgment required. When young adults used left parietal cortex (physical size task), older adults recruited parietal cortex on the right and when young adults used right parietal cortex (number magnitude task), older adults recruited parietal cortex on the left.

Age-related parietal recruitment has been reported in previous studies and has typically been assumed to reflect greater engagement of top-down attentional processes and increased dependence on resolving conflict in older adults, relative to their young counterparts. Previous studies have shown age-related increases in PPC activity in varied tasks, especially under demanding conditions. For example, greater bilateral PPC activity in older adults was reported in a primarily left-lateralized color-word Stroop task that involved filtering out distracting irrelevant information (Langenecker et al.,

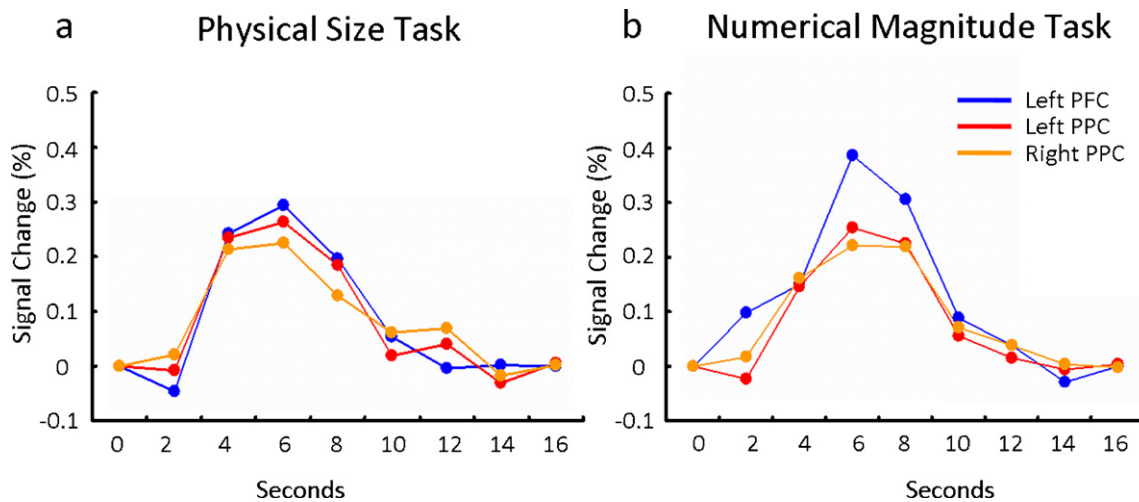


Fig. 7. The trial-averaged time-course of compensatory activity. Timecourses obtained from incongruent trials in the physical size task (a) and numerical magnitude task (b) for older participants. Timecourses are displayed for each region in which age-related compensatory activation was observed: left prefrontal cortex (PFC), left posterior parietal cortex (PPC), and right PPC.

2004; Milham et al., 2002; Prakash et al., 2009; Zysset et al., 2007), and in a primarily right-lateralized Go/No-go task that involved response inhibition (Nielson, Langenecker, et al., 2002; Nielson et al., 2004; Vallesi et al., 2011). This is the first study that demonstrates that older adults flexibly activate additional parietal cortex from either the left or right hemisphere, depending on the stimulus judgment required.

Importantly, we also found evidence that greater age-related contralateral parietal recruitment actually improved behavioral performance. The location of parietal activity that was associated with better performance depended on the task: in the number magnitude task, age-related recruitment of left posterior parietal cortex was associated with better performance whereas in the physical size task, age-related recruitment of right posterior parietal cortex was. These results are consistent with the hypothesis that age-related contralateral parietal recruitment compensates for neural decline and bolsters behavioral performance and moreover, that it is domain-specific (i.e., the pattern of age-related compensatory recruitment depends on the task).

Findings from a few previous studies are consistent with the hypothesis that age-related parietal recruitment can be compensatory although none have reported evidence for age-related parietal compensation that is specific to particular tasks. Fera et al. (2005) reported greater parietal activity in older adults in a probabilistic category learning weather prediction task and also reported parietal activity that was correlated with better behavioral performance in older adults. This study only examined one task and therefore does not speak to the issue of task-dependent or task-independent age-related neural recruitment. Recently, Heuninckx et al. (2008) reported that greater age-related activity in left superior parietal cortex was associated with better performance in a complex interlimb coordination task, but again only one task was studied and so task-dependent changes could not be examined. Finally, Davis et al. (2008) examined age-related effects on neural activity in both an episodic retrieval and visual perception task. They reported a positive correlation between age-related parietal recruitment utilizing composite performance across both tasks, but did not examine task-specific compensatory effects.

To summarize, our study shows that older adults recruit parietal cortex bilaterally when young adults show unilateral recruitment, that this additional recruitment is specialized and task-specific, and that this recruitment is compensatory in the sense that it is associated with better task performance.

We also isolated frontal regions that were overrecruited by old relative to young. In particular, we found a left inferior frontal region that was recruited by the older subjects across both the physical size task and the numerical magnitude task, and that was related to better behavioral performance. Increased activity in PFC regions, especially in left inferior frontal regions, has been frequently reported in older adults compared to young adults in tasks requiring response inhibition (Nielson et al., 2002; Vallesi et al., 2011) and resolving interference (Langenecker et al., 2004; Milham et al., 2002; Prakash et al., 2009; Wood et al., 2009; Zysset et al., 2007). The current study confirms these findings and demonstrates the relationship of the activity to better behavioral performance in healthy older adults.

The present findings in PFC activity are consistent with the Compensation-Related Utilization of Neural Circuits Hypothesis (CRUNCH) proposed to account for patterns of PFC overrecruitment in older adults (Cappell, Gmeindl, & Reuter-Lorenz, 2010; Reuter-Lorenz & Cappell, 2008; Reuter-Lorenz & Park, 2010; Schneider-Garces et al., 2010). The CRUNCH model posits that older adults recruit more neural resources (and therefore exhibit greater activity) at lower levels of cognitive demand than young adults, leaving fewer resources for higher levels of demand (therefore exhibiting equivalent or even lower activity). In the present study, as shown in Table 5, older adults elicited greater PFC activity bilaterally for the less demanding task (i.e., physical size task) compared to young adults, whereas older and young adults showed equivalent PFC activity for the more demanding task (i.e., numerical magnitude task).

Although the main point of this study was to investigate age-related neural compensation in the parietal cortex, there is one aspect of the behavioral results that is worth mentioning: The size of the interference effect was not significantly larger in the older subjects than in the younger subjects. Some previous studies have reported a significant increase in interference with age and have interpreted it as evidence for an age-related deficit in inhibitory function (Hasher & Zacks, 1988; Spieler, Balota, & Faust, 1996). On the other hand, a number of other studies have failed to find a significant interaction between age and congruity, as we did. For example, Langenecker et al. (2004) reported no age differences in the size of the congruity effect in a Stroop color-word fMRI task (both for reaction time and accuracy) and similar behavioral results were reported in other fMRI studies using Stroop-like paradigms (e.g., Mathis, Schunck, Erb, Namer, & Luthringer, 2009; Milham

et al., 2002; Schulte et al., 2009; Wood et al., 2009; Zysset et al., 2007; but see Prakash et al., 2009, for another paper that did report an age \times congruity interaction). Furthermore, in a meta-analysis of numerous studies, Verhaeghen and De Meersman (1998) concluded that the interference effect in the Stroop task is not age sensitive, and that apparent increases in interference in older subjects are actually a side effect of general slowing. We would not go so far as to argue that our results disconfirm the hypothesis that aging is associated with a deficit in inhibition, but will simply say that they are consistent with the general slowing hypothesis. It is also worth pointing out that the fact that the congruity effect was comparable in the two age groups indicates that the observed age differences in neural activity (both PFC and PPC) were not confounded by age differences in reaction time.

Finally, a crucial question is what cognitive functions are the compensatory activations performing? Although it can be difficult to make detailed inferences about cognitive processes from neuroimaging activations, we can offer a few general comments on the question. First, at the highest level, we can ask whether the additional regions recruited by the older subjects are performing the same, or different, functions as the regions used by the young subjects. Our guess is that they are performing the same functions, for four reasons. First, the time-course of activity in the additionally recruited regions is very similar to the time-course of activity in the regions used by the young (see Fig. 7). Second, in the only previous study we know of that investigated strategy use and age-related parietal recruitment (Fera et al., 2005), no age differences in strategy use were observed. Of course, their task was quite different so that evidence is admittedly weak. Third, regions of additional recruitment were in similar regions to those activated in the young, but in the contralateral hemisphere. If a completely different process were being used by the elderly, then one might expect the neural activity to be in very different regions. Fourth, different regions of additional recruitment were observed for the two different tasks, consistent with the idea that the activity reflected task-specific processing rather than some more general function that could be used as a compensatory mechanism across tasks.

We can also ask what specific cognitive processes were being performed in the regions of additional recruitment. Answering that question is even harder. The only thing we can say is that the processes are likely to be task specific, given that the neural activity was task-specific. Thus, we would speculate that additional recruitment in the right PPC during the physical size task reflects some aspect of size comparison and that additional recruitment in the left PPC during the numerical magnitude reflects some aspect of numerical processing. Future studies could use eye-tracking to gain insight into the specific strategies adopted by participants. Another idea would be to impose a time limit on responses to investigate whether behavior is affected and whether compensatory activity is still observed.

In closing, our major findings suggest that age-related over-recruitment is not restricted to prefrontal cortex, but extends to posterior parietal cortex. Like age-related recruitment of left PFC, recruitment of PPC also appears to be compensatory and predicts an improved ability to resolve interference in older adults. Unlike age-related recruitment of left PFC, however, we found evidence of task-specific age-related recruitment in PPC, with opposite hemispheres being recruited for the physical size and numerical magnitude tasks. We also found evidence for task-independent age-related recruitment in left PFC which was also associated with better performance across both tasks.

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