Contextual interference in recognition memory with age

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Previous behavioral research suggests that although elderly adults' memory benefits from supportive context, misleading or irrelevant contexts produce greater interference. In the present study, we use event-related fMRI to investigate age differences when processing contextual information to make recognition judgments. Twenty-one young and twenty elderly incidentally encoded pictures of objects presented in meaningful contexts, and completed a memory test for the objects presented in identical or novel contexts. Elderly committed more false alarms than young when novel objects were presented in familiar, but task-irrelevant, contexts. Elderly showed reduced engagement of bilateral dorsolateral prefrontal cortex and anterior cingulate relative to young, reflecting disruption of a cognitive control network for processing context with age. Disruption occurred for both high and low-performing elderly, suggesting that cognitive control deficits are pervasive with age. Despite showing disruption of the cognitive control network, high-performing elderly recruited additional middle and medial frontal regions that were not recruited by either low-performing elderly or young adults. This suggests that high-performing elderly may compensate for the disruption of the cognitive control network by recruiting additional frontal resources to overcome cognitive control deficits that affect recognition memory.
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In the present study, we investigate age differences in neural activations when background contexts support or interfere with recognition judgments of objects. Relative to young adults, elderly adults may be disproportionately influenced by context. When participants study nouns in sentence contexts that are either consistent or irrelevant to the noun's meaning, the effects of age are magnified (Earles et al., 1994). Compared to a neutral context condition, older adults' memory for nouns improves as much, or more than, young adults' for the consistent contexts, but when the nouns appear in irrelevant, or distracting, contexts, older adults' memory is disrupted disproportionately. This finding is consistent with Hasher and Zacks' (1979) view that some contextual information is processed automatically, and thus is unaffected by aging. However, inhibition failures could allow context to be processed at the expense of item information (Hasher and Zacks, 1988). Recent neuroimaging data suggest that this may be the case, with older adults focusing disproportionately on backgrounds. Older adults activate neural areas in the ventral visual cortex associated with processing background scenes at the expense of object processing regions (Chee et al., 2006).

One prediction that follows from the observed age differences in the neural response to objects but not backgrounds is that older adults may disproportionately utilize viewed background information in making memory judgments, compared to young adults. We test this prediction in the present study by having younger and older adults encode objects placed on background contexts. Participants subsequently make recognition decisions for the objects, and are instructed to ignore backgrounds in making their decisions. The critical condition occurs when a novel object is placed on a background that has been studied previously. If object encoding is impaired with age, as suggested by Chee et al. (2006), backgrounds should play a dominant role in informing elderly adults' recognition decisions. Older adults should be disproportionately influenced by background context relative to young adults during recognition, leading them to commit more false alarms to novel objects when the background is familiar.

Our definition of context as supporting background scenes diverges from the manipulations commonly employed in the source memory literature. Meaningful environmental contexts, such as background scenes, differ from many source features in that contexts add semantic information to the interpretation of the object such that background context cannot be arbitrarily changed without altering the meaning of the object. For example, whether a lion has a jungle or a circus as its background leads to different interpretations of the object itself. In contrast, source memory studies typically investigate memory for a single feature that is not necessarily intrinsically or semantically related to the target item (e.g., remembering the color or spatial location in which a picture

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of an object was studied). Older adults exhibit disproportionately poorer memory for source features than target information (Hashtroudi et al., 1989; Johnson et al., 1993; Spencer and Raz, 1995), including the color of an item (Park and Puglisi, 1985), the voice in which an item is presented (Kausler and Puckett, 1981), and the spatial location of an item (Park et al., 1982; Perlmutter et al., 1981). Although there are few studies of memory for objects presented in complex background contexts, the available evidence suggests that older adults remember context more poorly than young, but unlike the disproportionate declines in source memory, the decline in context memory with age is proportional to the decline in object memory (Park et al., 1986, 1984). It is also clear that meaningful background context can play an important role in facilitating target memory, as the presence of a rich environmental or semantic context at encoding generally supports accurate judgments for both old and young adults when it is re-presented at recognition (e.g., Bayen et al., 2000; Naveh-Benjamain and Craik, 1995; Park et al., 1984, 1986, 1987; Puglisi et al., 1988; Smith et al., 1990), as would be predicted by the encoding specificity effect (Tulving and Thomson, 1973). Although many studies show equivalent contextual encoding by the young and elderly, there are some that demonstrate that the elderly rely on context even more than young adults (e.g., Park et al., 1990; Smith et al., 1998). The re-presentation of rich background information studied at encoding may enhance feelings of familiarity at recognition. Familiarity traces can support memory because they operate automatically and are intact with age (Jacoby, 1991; Jennings and Jacoby, 1993; 1997; but see Duarte et al., 2006).

The present study investigates the neural circuitry activated when young and old adults make recognition judgments for objects in the context of familiar backgrounds. We hypothesize that presenting an unstudied object in a familiar context at recognition will create a conflict between the novel item and familiar context, and that subjects will rely on top-down monitoring and control mechanisms to override feelings of familiarity to correctly reject the novel object. However, cognitive control is compromised by aging (Braver and Barch, 2002; Braver et al., 2001, 2005). Thus, we predict that older adults will fail to engage cognitive control to override familiarity traces from backgrounds, leading to an increase in false alarms to novel objects when backgrounds are familiar from prior study. We expect that these recognition errors will reflect decreased engagement of frontal cognitive control regions by older adults. Previous research identifies dorsolateral prefrontal (Milham et al., 2002), inferior prefrontal (extending into dorsal regions on the left; Persson et al., 2004), and anterior cingulate (Persson et al., 2004) cortex as important to cognitive control, and affected by aging. Although the tasks employed by these previous studies tap working memory and executive functions, we predict that these same regions will be implicated in age-related deficits in cognitive control in *long-term* memory.

Materials and methods

Participants

Twenty-one young adults (ages 18–28; 10 males) from the University of Illinois at Urbana-Champaign and 20 community-dwelling elderly adults (ages 60–84; 6 males) from the surrounding communities participated in the study. Participants were screened for fMRI eligibility, including right handedness, English as a native language, good neurological, psychological, and physical health,

the absence of medications or conditions that could affect cognition or blood flow, and the lack of other contraindications that would preclude participation in the study. All participants scored at least at a 27 (out of 30) on the Mini-Mental State Examination (MMSE; Folstein et al., 1975), suggesting that the elderly sample did not evidence dementia. Participants provided written informed consent before beginning the study. The study procedures were approved by the University of Illinois Institutional Review Board.

Procedure

Neuropsychological measures

Participants completed several neuropsychological tests to compare cognitive ability across age groups, including Digit–Symbol coding (Wechsler, 1997a), a measure of speed of processing, forward and backward spatial span (Wechsler, 1997b), a measure of working memory, and the Information and Comprehension scales from the WAIS-R (Wechsler, 1981), measures of world knowledge. Table 1 presents education, health ratings, and performance on these tasks, indicating that the young performed better than the old on the speed and working memory measures, but the two groups were equated on measures of world knowledge, in line with the usual pattern of age-related cognitive declines.

fMRI session

Before scanning, participants were instructed on the task, and then completed encoding and recognition inside the scanner. Participants encoded 96 color photographs consisting of an object placed on a meaningful background. Pictures were presented across two runs, each lasting 4 min and 48 s, and were interspersed with a total of 48 baseline trials (i.e., fixation cross). During the 4 s each picture was presented, participants pressed a button to rate the pleasantness of the picture as either positive or negative/neutral. All pictures contained an object placed in a plausible context. Thus, there was no task manipulation during encoding, and the encoding data are not discussed further.

For the recognition task, participants were instructed to decide whether or not they recognized the *object* from the initial presentation of the pictures, and to respond with a "yes" or "no" keypress. Participants were warned that context backgrounds could be the same or different than those originally paired with the objects, and they should respond "yes" when the object was

Table 1
Performance of young and elderly on neuropsychological measures (means and standard deviations)

	Young	Elderly	*p*-Value
Age	21.05 (3.25)	68.10 (6.97)	0.000 *
Health rating [a]	4.23 (.94)	4.15 (.75)	0.74
Years of education	14.88 (2.35)	14.97 (2.21)	0.90
Digit–symbol	72.43 (10.65)	51.35 (13.04)	0.000 *
WAIS information	21.57 (4.30)	22.55 (3.35)	0.42
WAIS comprehension	20.86 (3.35)	22.50 (4.57)	0.20
Mini-mental	29.14 (.85)	29.30 (.80)	0.55
Forward spatial span	10.00 (1.79)	7.95 (1.73)	0.001 *
Backward spatial span	9.90 (1.51)	7.05 (1.47)	0.000 *

[a] Health was self-rated on a 5-point scale. A rating of 4 = better than average.

* $p < 0.001$.

Encoding
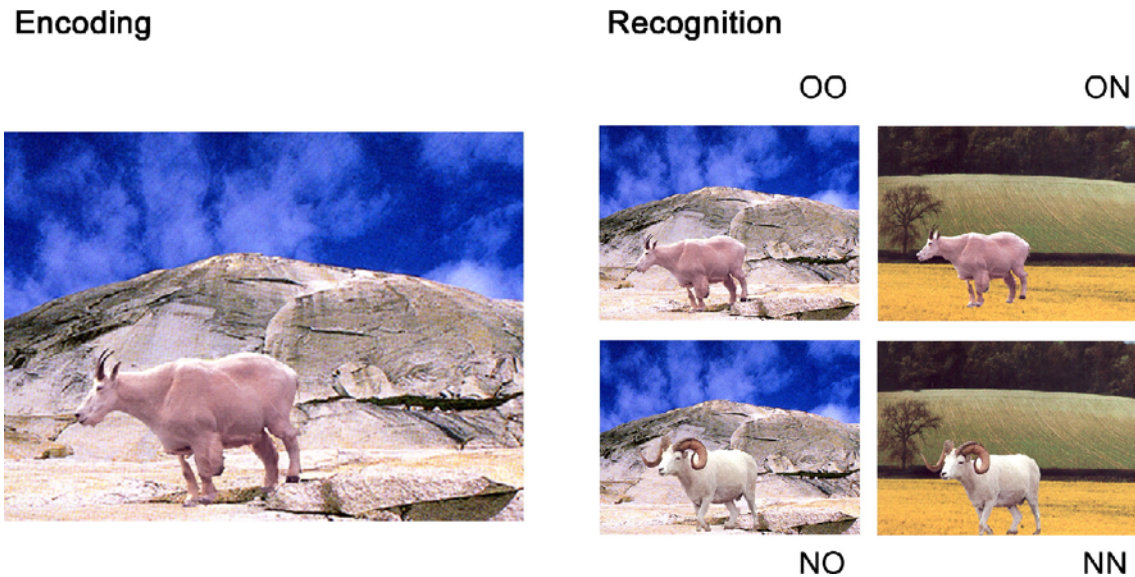
Recognition

OO   ON

NO   NN

Fig. 1. Example recognition picture stimuli. Each picture consists of an object placed on a meaningful background. At recognition, the object and background independently can be either old, that is, identical to one presented at encoding, or new. The object's classification as either Old or New is denoted by the first letter in each condition name, and the background's classification is denoted by the second letter (e.g., a novel object on a previously studied background is denoted NO).

recognized from the first portion of the study, regardless of the background. Pictures were presented for 4 s each, interspersed with 96 baseline trials in a jittered design with ISI varying between 0 and 12 s. Trials were presented across four runs, each 4 min, 48 s long. Images were presented using E-prime software (Psychology Software Tools, Pittsburgh, PA) and back-projected onto a screen outside of the magnet.

There were 192 recognition trials, comprised of four different picture types which are displayed in Fig. 1. Forty-eight of the pictures consisted of an Old object against an identical Old background (OO pictures). Forty-eight of the pictures contained an Old object against a New background (ON pictures). Because both of these types of stimuli contain an old object, participants should respond "yes" to denote that the object was presented previously. In contrast, participants should respond "no" to the 96 new object trials, regardless of whether the New object was presented against an Old previously encoded background (NO pictures) or against a New background (NN pictures). Using this naming convention, the first letter corresponds to the object (*New* or *Old*), while the second letter corresponds to the background.

Image acquisition

Participants were scanned in a 3 T Siemens Magnetom Allegra MR headscanner (Siemens, Erlangen, Germany). Images were acquired using a gradient-echo EPI sequence with a TR of 2000 ms, a TE of 25 ms, a FA of 80°, a FOV of 22 cm, and a 64×64 matrix. 32 oblique axial slices, 4 mm thick (with 0.4 mm gap between slices), were acquired approximately parallel to the AC–PC line. High-resolution coplanar MPRAGE anatomical images were also obtained.

Data analysis

SPM2 (Wellcome Department of Cognitive Neurology, London, UK) was used to process functional images that were slice-time corrected, realigned to correct for motion, normalized to a common stereotactic system (MNI), resampled to 2-mm cubic voxels, and smoothed using a 5-mm Gaussian kernel. The contrast images were smoothed with an 8-mm Gaussian kernel for a total effective smoothing of approximately 9 mm.

Each individual's data were modeled with separate regressors for correct and incorrect responses to the four picture types (OO, ON, NO, and NN). Inferences from the model were based only on correct responses. To isolate the impact of context familiarity on neural activations, the New/New items (NN) were subtracted from the New/Old items (NO), as this contrast isolates subjects' unique response to the conflict created when a subject is presented with a novel object in a familiar context and should reject the object as never presented. This contrast is the basis for the results reported here.[1] To assess age differences in neural activations, we conducted a two-sample random effects group analysis of young participants versus elderly.

In addition to the comparison of age groups, we also examined differences between high- and low-performing elderly and relied on a two-sample random effects group analysis. For this analysis, a median split on A′ scores was used to assign elderly participants to the high or low performer groups. A′ is a nonparametric measure of recognition discrimination that incorporates hit and false alarm rates into a single measure (Snodgrass and Corwin, 1988). To calculate A′ scores, we used the hit rate for OO pictures and the false alarm rate for NO pictures (see Stanislaw and Todorov, 1999 for formulas). By incorporating hit and false alarm rates, A′ isolates memory discriminability from response bias (i.e., the tendency to respond "yes" or "no"). This A′ score was used to distinguish high from low performers because it is the most sensitive measure of correct object discrimination, determining a subject's ability to discriminate an old target from a never-presented one when the

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[1] We also tested for age differences in the comparisons of OO−ON pictures and OO−NO pictures, and noted minimal differences between the groups. These comparisons are shown in Supplementary Figs. 1 and 2.

context is familiar in both cases.[2] All group comparisons were thresholded at a $p < 0.001$ (uncorrected for multiple comparisons) and a spatial extent >64 voxels. The cluster extent threshold was determined on the basis of Monte Carlo simulations to achieve an overall multiple comparisons correction of $p < 0.05$ (Slotnick, 2005).

Region of interest analysis

To characterize the response of the regions in each group, we conducted region of interest analyses by extracting the average difference of the betas (parameter estimates of MR signal) for the NO and NN conditions (accurate trials only) using masks created with MarsBaR (Brett et al., 2002). Each region was centered on a group-level activation peak, and constrained to a sphere of 10-mm radius. Out of the significant peaks, we focused on prefrontal regions because previous literature has identified a significant role for these regions in context processing (Burgess et al., 2001; Cabeza et al., 2003; Hayes et al., 2004) and in cognitive control (Braver et al., 2001; Milham et al., 2002; Persson et al., 2004). In addition, the effects of aging are often more prominent in prefrontal regions (Cabeza et al., 2000, 2002). For the comparison across age groups, ROI masks were centered on our peak activations at the following MNI coordinates: left (−40, 2, 34) and right (40, 18, 26) dorsolateral prefrontal cortex, anterior cingulate cortex (0, 20, 48), and left anterior prefrontal cortex (−24, 50, 8). We also queried these regions to examine whether the age differences were present to the same extent in high- and low-performing elderly. For the comparison of regions distinguishing high- and low-performing elderly, ROIs were selected from our peaks in the medial superior prefrontal region (20, 62, −4) and a right middle frontal region (40, 58, 12). The middle frontal gyrus is a candidate compensatory region identified in prior literature (Cabeza et al., 2002; Gutchess et al., 2005). The medial prefrontal cortex has also demonstrated age-related differences in long-term memory tasks, although the nature of the region's contribution to age differences in behavior is less clear (Gutchess et al., 2005).

Results

Behavioral data

Recognition performance

To assess the impact of aging on recognition memory under conditions of conflict, we separately analyzed hit rates (correct recognition of previously presented objects) and correct rejection rates (correct rejection of novel objects) across the four conditions. Results are displayed in Fig. 2 and demonstrate, overall, that elderly adults had difficulty rejecting a novel object when it was presented in a familiar background, as we had hypothesized. Because there are two types of hits (correct responses to Old/Old or Old/New items) and two types of false alarms (incorrect response to New/Old or New/New items), the data cannot be fully summarized by a

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[2] The fMRI analyses focus on the response to new items, which may suggest that false alarm rates would be the most appropriate measure to discriminate high from low performers. However, the false alarm rate alone does not reflect memory discrimination, but is largely influenced by response bias. Empirical investigation of the elderly adult data shows that the false alarm rate (to NO) has a *positive* correlation with the hit rate (to OO) ($r = 0.44$, $p = 0.05$), and is more strongly correlated with response bias ($r = -0.85$) than with the discrimination measure of A′ ($r = -0.53$).
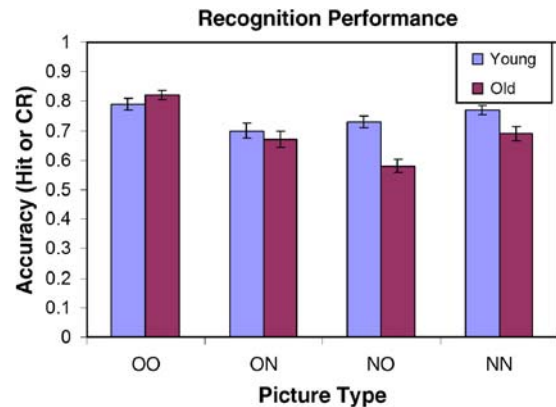

Fig. 2. Picture recognition performance by young and elderly. Bars depict hit rates for the OO and ON stimuli, and correct rejection (CR) rates for the NO and NN stimuli. Although age differences are not apparent for the hit rates, older adults perform worse than younger adults on correct rejections. The age difference is most pronounced for the NO items, in which novel items placed on a familiar background must be rejected.

single A′ score. Furthermore, the primary comparisons of interest are the difference in hit rates when an object must be recognized while set in an unfamiliar context compared to when an object occurs in a previously encountered context (ON versus OO), and the difference in false alarm rates when a familiar context must be rejected, compared to a novel context (NO versus NN). For hit rates to previously seen objects, we conducted a 2×2 mixed analysis of variance (ANOVA), with Age (young/elderly) as a between-subject variable and Background (Old/New) as a within-subject variable. The analysis revealed a main effect of background ($F(1,39) = 56.64$, $p < 0.001$), such that hit rates were higher when the old object was presented with its original background ($M = 0.80$) compared to a new background ($M = 0.69$). There was a marginal interaction of Age × Background ($F(1,39) = 3.09$, $p < 0.09$), but the main effect of age did not approach significance ($F < 1$).

In the comparison of correct rejection rates for novel objects, the age groups differed substantially, particularly for the NO condition. We conducted a 2×2 mixed analysis of variance (ANOVA), with Age (young/elderly) as a between-subject variable and Background (Old/New) as a within-subject variable. The background presented at retrieval significantly impacted object recognition ($F(1,39) = 26.70$, $p < 0.001$), making it more difficult to reject a novel object when it was tested on a familiar ($M = 0.66$), as opposed to a novel ($M = 0.73$), background. In contrast to the hit rate data, there was a main effect of age ($F(1,39) = 21.61$, $p < 0.001$), with elderly correctly rejecting fewer items ($M = 0.64$) than young ($M = 0.76$). The main effects were qualified by a significant interaction of Age × Background ($F(1,39) = 5.32$, $p < 0.03$), with the elderly exhibiting a greater impairment relative to the young when the backgrounds were familiar (NO condition). The interactions show that the elderly, as we hypothesized, are disproportionately impaired at correctly rejecting the NO pictures relative to the NN pictures, and that this impairment occurs above and beyond any general tendency to make fewer correct rejections with age.

Reaction times

To assess the impact of cognitive control demands on age differences in reaction times, median reaction times for each

participant were computed for each of the four conditions using correct trials (Table 2). We conducted separate 2×2 mixed analyses of variance (ANOVA) for hits and correct rejections, with Age (young/elderly) as a between-subject variable and Background (Old/New) as a within-subject variable. For reaction times to hits, the analysis revealed a main effect of background ($F(1,39)=7.77$, $p<0.01$), such that responses were faster for ON ($M=1569$ ms) than OO ($M=1718$ ms) hits. The main effect of age was also significant ($F(1,39)=4.24$, $p<0.05$), with the young ($M=1524$ ms) faster than the elderly ($M=1763$ ms), but the interaction of age × background did not approach significance ($F<1$).

For reaction times for correct rejections of novel objects, the main effect of age was significant with younger adults ($M=1337$ ms) responding faster than older adults ($M=1519$ ms), $F(1,39)=5.63$, $p<0.05$, but there was only a trend for a main effect of background ($F(1,39)=2.48$, $p=0.12$), with responses to NN trials ($M=1409$ ms) slightly faster than to NO trials ($M=1448$ ms). Unlike the recognition memory data, the interaction did not reach significance for reaction times. The marginal interaction of Age × Background ($F(1,39)=3.73$, $p<0.06$), suggests that the young were somewhat faster in the NN trials relative to the NO trials, whereas the elderly showed similarly high reaction times in both conditions. We were surprised by this finding, as we would have expected the difficulty the elderly experienced in the NO condition to be reflected in slower performance in the NO condition compared to the NN condition. We note that the elderly show considerable variability in these conditions relative to the young, even when taking into account their slower RTs, and thus the RT data may be somewhat insensitive to this manipulation. It is also possible that the young take longer to recruit cognitive control mechanisms in the NO condition in order to successfully reject novel objects but that the elderly are unable to successfully engage cognitive control mechanisms for the NO trials, in which case the RTs would not differ between NO and NN trials for elderly, just as we observed. Because the study was designed to focus on memory and the primary measure of interest is recognition performance, we note the unexpected pattern of reaction time data and focus our attention on the memory measure for the behavioral data.

fMRI data

Age differences in the rejection of novel objects in familiar contexts

The NO versus NN contrast identified a number of regions where the young showed greater activation than the old, consistent with our prediction of cognitive control failures with age (Fig. 3A). As shown in Table 3A, the majority of these regions were located in prefrontal cortex, including left and right dorsolateral prefrontal cortex, left anterior middle frontal gyrus, and anterior cingulate cortex, although there were some posterior activations (i.e., posterior cingulate, left calcarine/lingual gyrus, and left angular/middle temporal gyrus). The extensive age-related differences in the activation of dorsolateral and anterior cingulate regions suggest

that the young, more than the elderly, showed disproportionate engagement of a cognitive control network when confronted with a novel object presented in a familiar context. This network involves dorsolateral prefrontal regions (DLPFC) (Braver and Barch, 2002; Buckner, 2003) and anterior cingulate cortex (ACC) (Milham et al., 2002). The NO condition required participants to overcome feelings of familiarity when confronted with the old background, and reject the novel object. This was more difficult for the elderly than the young as shown by the older adults' recognition memory performance and the neural data indicate that they showed less engagement of the cognitive control network than young adults.

The cognitive control deficits are selective to rejecting novel objects paired with familiar, as opposed to novel, contexts. The comparisons of OO versus ON (Supplementary Fig. 1) and OO versus NO (Supplementary Fig. 2) do not reveal age differences, suggesting that older adults are not impaired whenever there is conflict between novel and familiar information (which would be true for the supplemental analyses, as well as NO versus NN). Rather, the age differences are specific to the case when cognitive control is required to reject lures with familiar *context* (which is true for NO versus NN).

In order to assess the contribution of these cognitive control regions to long-term memory, we assessed the relationship between memory performance (as assessed by an A′ score using OO scores as the hit rate and NO scores as the false alarm rate) and the amount of activation in prefrontal regions (assessed by the parameter estimate for NO−NN). See Footnote 2 for a justification for using A′ as our measure of performance. Whereas memory performance did not correlate with the amount of activation for young adults, older adults with higher memory performance activated the DLPFC more than poorer performing elderly, as assessed with Pearson's correlations (Young: left: $r=-0.03$, and right$=0.08$; Elderly: left$=0.52$, $p<0.05$, and right$=0.57$, $p<0.01$). Surprisingly, the ACC and anterior prefrontal (BA 10) regions of interest were unrelated to memory performance for the young (ACC: $r=-0.07$; anterior PFC: $r=0.00$) and elderly (ACC: $r=0.31$, $p=0.18$; anterior PFC: $r=0.35$, $p=0.14$). These findings are reminiscent of those of Persson et al. (2004), who also reported deficits in lateral prefrontal regions with age for tasks requiring high levels of cognitive control, but interpreted impaired ACC activation as reflecting general resource limitations with age, regardless of cognitive control demands. Based on evidence that BA 10 governs more specific recognition judgments (Ranganath et al., 2000), age differences in the region could reflect age differences in retrieval orientation, such that the young attend more to the specific perceptual details of the NO pictures whereas the elderly rely on more general, or gist-based, recognition processes (Koutstaal et al., 1999). Although these orientations could differ across age groups, the processes do not distinguish higher from lower accuracy within an age group.

Performance differences for high- and low-performing elderly adults

The previous analyses reveal different relationships between DLPFC and memory performance across the age groups, but do not fully characterize the role of DLPFC for high- and low-performing elderly and young adults. If cognitive control is disrupted widely across subgroups of elderly (Braver et al., 2005), then activation of DLPFC should also be impaired. However, some previous studies have suggested that compensatory mechanisms can support equivalent performance in high-performing elderly and

Table 2
Means and standard deviations for reaction times (milliseconds) for hit and correct recognition responses

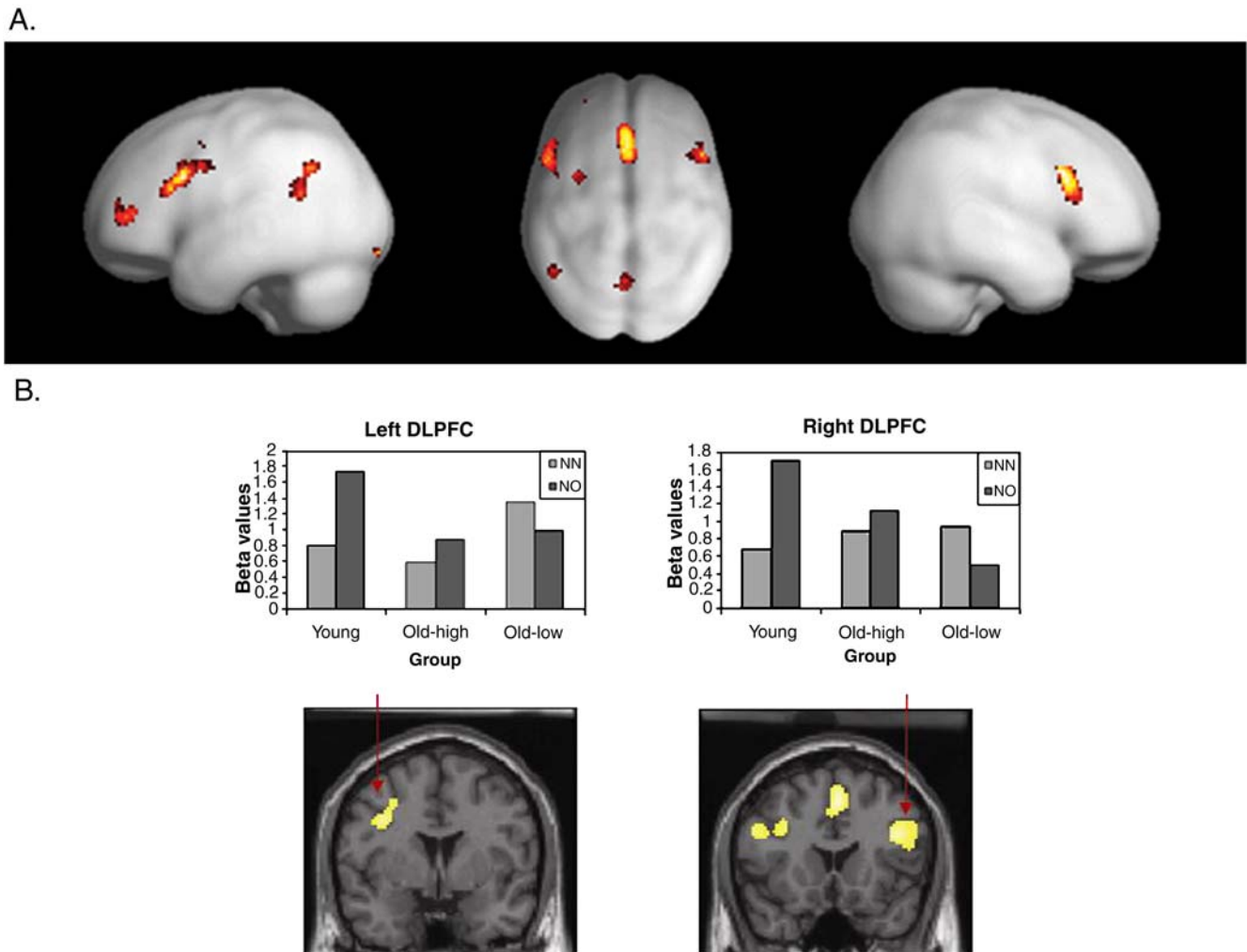|	OO	ON	NO	NN
Young	1597 (440)	1451 (260)	1380 (180)	1294 (182)
Elderly	1840 (536)	1687 (355)	1515 (295)	1524 (342)

A.

B.

Fig. 3. (A) Age differences in neural activation. Group differences are displayed for the contrast of New object Old background (NO) pictures minus New object New background (NN) pictures. Differences are displayed as *t*-values for Young subjects minus Elderly subjects, displayed at a threshold of $p < 0.001$ (uncorrected) and a cluster extent threshold of 64 voxels (equivalent to a corrected $p < 0.05$). Age differences are prominent in prefrontal regions, including bilateral DLPFC and anterior cingulate, and also occur in posterior regions, including precuneate, lingual, and inferior parietal gyri. Note that age differences were not present for the reverse subtraction (Elderly minus Young). (B) Group differences in DLPFC. Coronal sections highlight the peaks for age differences in DLPFC. As seen in the graphs, young adults show the largest difference in the parameter estimates for NO and NN, and the pattern differs significantly from both groups of elderly across both regions. High-performing elderly differ significantly from low-performing elderly in right DLPFC and marginally in left DLPFC.

young through the engagement of unique neural regions (Cabeza et al., 2002; Rosen et al., 2002). We evaluated the extent of age differences in memory performance and neural activation patterns across high- and low-performing elderly, relative to the young, and also assessed the potential for compensatory activation in high-performing elderly.

Using a median split on A′ scores for elderly, we observed that both age and level of recognition performance in older adults are associated with cognitive control decrements in long-term memory. High-performing elderly ($M = 0.83$) recognized pictures as well as young adults ($M = 0.84$), $t < 1$. Low-performing elderly ($M = 0.76$) had significantly lower A′ scores than the young, $t(29) = 3.69$, $p < .001$, and high-performing elderly, $t(18) = 5.01$, $p < 0.001$. Even though behaviorally we do not see evidence for widespread age impairments in cognitive control, high-performing elderly differ neurally from young adults in left and right DLPFC (see Fig. 3B):

left DLPFC $t(29) = 2.11$, $p < 0.05$; right DLPFC $t(29) = 2.16$, $p < 0.04$. Young adults show greater DLPFC activation for NO trials compared to NN trials. High-performing elderly activate in the same direction as the young (NO > NN), but high-performing elderly distinguish the conditions significantly less in DLPFC than the young: left DLPFC $t(29) = 2.11$, $p < 0.05$; right DLPFC $t(29) = 2.16$, $p < 0.04$. Furthermore, low-performing elderly exhibit a reversal from the pattern seen for the other two groups, with more DLPFC activation to NN than NO pictures. High- and low-performing elderly differ significantly in right DLPFC ($t(18) = 2.23$, $p < 0.04$), and marginally in left DLPFC $(t(18) = 1.96$, $p < 0.07$).

Overall, this pattern suggests that the dorsolateral prefrontal regions respond less when cognitive control is needed with age, and that further dysfunction occurs for low-performing elderly. This suggests that there are age-related neural changes to the

Table 3
MNI coordinates of regions exhibiting significant group differences in the contrast of NO − NN pictures, using a threshold of $p < 0.001$ (uncorrected)

| Region	Hemisphere	Coordinates of activation peak (x, y, z)			BA	t Value
A. Young − Elderly						
Anterior cingulate/medial PFC	Medial	0	20	48	32/8	4.26
Dorsolateral prefrontal	L	−40	2	34	44	3.88
	R	40	18	26	46	4.13
Middle frontal gyrus	L	−24	50	8	10	3.91
Lingual gyrus	L	−4	−86	−12	18	4.27
Precuneus	L	−2	−64	40	7	4.11
Inferior parietal	L	−44	−50	22	22	4.00
Middle orbitofrontal	R	14	10	−10	25	4.70
B. High − low-performing elderly						
Superior frontal	R	20	62	−4	10	6.00
Middle frontal gyrus	R	40	58	12	10	5.13
Inferior frontal	R	52	32	0	47	5.55
	L	−38	24	−8	47	5.11
Middle temporal	L	−66	−40	0	21	4.49
Superior temporal	R	60	−62	28	39	4.28

Labels correspond to the peak activated voxel.

cognitive control network that apply across the board irrespective of memory performance.

If this is so, how are high-performing elderly able to match behaviorally the performance of their younger counterparts? This question motivated the search for 'compensatory regions' in high-performing elderly. We found several prefrontal areas that showed greater differential activation between NO and NN in the high-performing elderly compared to low-performing elderly (Table 3B). These areas were the medial superior frontal (BA 10; MNI coordinates 20, 62, −4) and middle frontal regions (BA 10; MNI
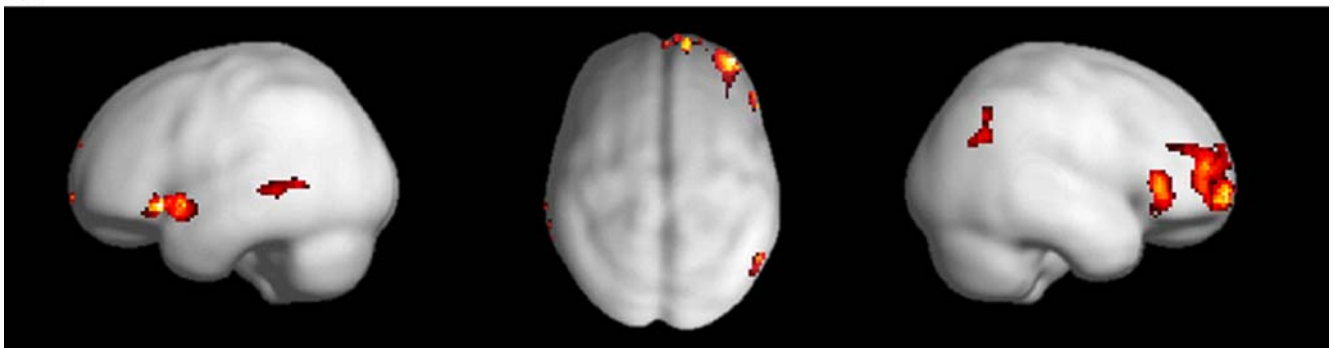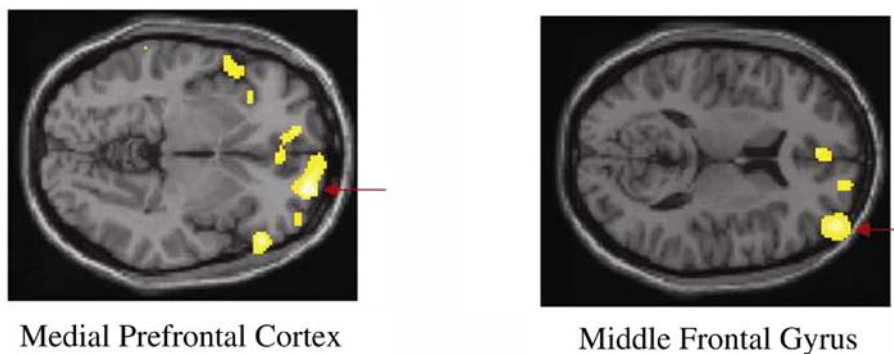

Fig. 4. (A) High versus low performer differences for elderly participants. Group differences are rendered for the contrast of New object Old background (NO) pictures minus New object New background (NN) pictures. Differences are displayed for high-performing elderly minus low-performing elderly, displayed at a threshold of $p < 0.001$ (uncorrected) and a spatial extent >64 voxels. The increased activations for high-performing elderly adults are located primarily in right prefrontal regions. Note that age differences were not present for the reverse subtraction (Low performers minus High performers). (B) Group differences in prefrontal cortex. Axial slices highlight the peaks in medial and middle prefrontal regions.

coordinates 40, 58, 12) (Figs. 4A and B). Notably, these regions did not differ in the overall comparison of young and elderly, suggesting that high-performing, but not low-performing, elderly may recruit additional regions to contribute to task performance. Previous studies have suggested that the elderly can recruit middle frontal gyrus in service of task monitoring (Cabeza et al., 2002; Gutchess et al., 2005). Medial prefrontal cortex, with its role in internal versus external orientation (Gusnard et al., 2001), could implicate another type of monitoring recruited by older adults.

There were no significant age differences in medial temporal activation in any of these analyses.

Discussion

In this study, we show that elderly adults are selectively poorer than the young at rejecting novel objects when the objects are placed in previously shown background contexts. Two experimental results support our hypothesis that this finding arises from deficits in cognitive control. First, we found that young adults, who were better than elderly at identifying objects as novel when these were placed in old backgrounds, showed higher activation of frontal cognitive control regions compared to elderly. Second, among the elders who showed better recognition memory we found greater engagement of a separate set of frontal control regions. These findings suggest that age-related impairments in cognitive control, previously identified in the domains of working memory and executive functioning (e.g., Braver et al., 2001, 2005; Milham et al., 2002; Persson et al., 2004), impact long-term recognition memory.

Interestingly, we identify a dissociation between behavioral failures of cognitive control, which are not present for the high-performing elderly compared to the young, and neural changes to the cognitive control network, which do affect the high-performing elderly. While this is generally consistent with findings of the age impairments in cognitive control (Braver et al., 2005), our data suggest that high-performing elderly can approximate the performance of the young by engaging unique neural regions, perhaps reflecting compensation. We posit that the additional regions contribute to increased monitoring of familiar context based on prior work implicating a role for these regions in monitoring (e.g., Cabeza et al., 2002). However, additional research is needed to establish whether the recruited regions support the detection and monitoring of conflict or the resolution of interference.

Our focus on the *correct rejection* of lures departs from the emphasis of previous studies on age differences for hits alone (correctly identifying an old item as old), or on correct rejections only in relationship to hits (e.g., Velanova et al., in press). These studies identify age differences in medial temporal regions that govern recollection and familiarity (Cabeza et al., 2004; Daselaar et al., 2006). By contrasting the neural response to partially familiar lures with that to entirely novel lures, we identify a role for cognitive control in long-term recognition memory. Critically, the age-related deficits in cognitive control are specific to the case in which familiar contexts must be rejected, and do not emerge during the recognition of familiar objects, even when they are presented in novel contexts.

Although we have discussed these effects as reflecting recognition processes, it is possible that the age differences in engaging cognitive control regions also reflect a failure of encoding processes. At encoding, older adults could encode the original item–context pairs more poorly than young adults due to

binding failures. Younger adults would thus be more aware of the mismatch in the NO condition at recognition, leading to higher correct rejection rates and stronger engagement of the cognitive control network. However, the binding failure hypothesis would seem to predict poorer performance for elderly adults relative to the young for both the ON and NO conditions. In the ON condition, young adults should be able to use the old object to access the bound representation of the original object–background pair. This would support the young adults' ability to correctly recognize the object as "old", regardless of the new background. For older adults, however, the ON trials should feel partially old and partially new, and without access to the bound representations, the novel information should lead older adults to mistakenly reject old objects as "new" more often than the young. Thus, binding failures would predict age differences in the ON condition, which is not the case in our data. Our data seem most consistent with the interpretation that age differences reflect a failure of cognitive control during recognition.[3]

One challenge for future work is to further validate the differences between high and low performers. Additional support for the individual differences reported here could be obtained through the use of independent measures to identify individuals with high or low levels of cognitive control. For example, a context working memory task (Braver et al., 2001, 2005; Braver and Barch, 2002) or a battery of cognitive control measures (Mather and Knight, 2005) might be expected to target the same control processes required by our task in order to reject novel objects in a familiar context.

Individual differences in attention to context could also be assessed using neural markers of suppression. Gazzaley et al. (2005) identify age-related deficits in the suppression of irrelevant information in working memory. In their study, the degree to which suppression occurs during encoding correlates with working memory performance in the elderly. We speculate that the older adults' difficulty in ignoring context would be apparent during working memory. During the encoding of objects, older adults would be expected to exhibit poor suppression of context-related activity, reflected by the activation of parahippocampal gyrus. Across individuals, poorer suppression of attention to backgrounds would contribute to poorer object encoding. Assessing the influence of irrelevant contexts on working memory with age would further bridge the present results with the encoding processes studied by Chee et al. (2006). Furthermore, identifying cognitive control failures in working memory might suggest that the age-related failures occur in initial gating processes, rather than later conflict resolution mechanisms. Although the present study is not designed to pinpoint the precise stage in which cognitive control failures occur with age, elderly adults' flat reaction times for the NO and NN conditions lead us to speculate that the failure could occur early in the detection and monitoring of conflict. If control processes failed in the conflict resolution stage, we might expect to find long reaction times in the NO condition as older adults attempt to resolve conflict.

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[3] The neural data also appear to be inconsistent with a binding failure explanation. Binding processes during both encoding of scenes (Chee et al., 2006) and recognition of re-presented word pairs (Giovanello et al., 2004) implicate the hippocampus, a region in which we did not find significant age differences in the present study. The functions of the regions that show age differences are consistent with a cognitive control explanation.

The main takeaway message from the present paper is that the elderly experience more difficulty in engaging a conflict resolution/cognitive control network than the young when confronted with a novel stimulus that should be rejected when it is placed in a familiar context. This finding, along with those of Chee et al. (2006), suggests that older adults are disproportionately biased to process context, and may be unduly affected by it. To the extent that context is interfering, it will have negative effects on older adults' object memory. The present findings suggest that the sometimes confusing behavioral effects associated with context and aging may be best understood in terms of the demands associated with context, as context effects sometimes show more facilitation for elderly, sometimes less, and sometimes are equally facilitative (see Craik and Jennings, 1992 for a discussion). We posit that if context is interfering and requires active engagement of a conflict monitoring network, it will be disproportionately negative in its effect on elderly. If context automatically activates networks that support memory (demonstrated behaviorally but not neurally by Park et al., 1990; Smith et al., 1998), then the effects may be disproportionately facilitative for elderly. Finally, context may have equivalent effects on the old and young when it neither misleads nor automatically activates supportive networks (as in Park et al., 1984, 1986, 1987; Puglisi et al., 1988; Smith et al., 1990). Much more research is needed to determine the legitimacy of this framework, but it provides a fertile ground for understanding the important role of nontarget information in biasing our judgments and behaviors with age.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2007.01.043.

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