Effects of aging on recognition of intentionally and incidentally stored words: An fMRI study

Frederik M. van der Veen⁎, Frouke A.P. Nijhuisb, Danielle J. Tisserandc, Walter H. Backesb, Jelle Jollesb

⁎ Department of Psychiatry, Erasmus Medical Centre, Rotterdam, P.O. Box 2040, 3000 CA Rotterdam, The Netherlands
b Brain and Behavior Institute, University of Maastricht, The Netherlands
c Rotman Research Institute, Baycrest Centre for Geriatric Care, Toronto, Canada

Received 30 August 2005; received in revised form 27 March 2006; accepted 2 April 2006

Available online 6 June 2006

Abstract

Functional magnetic resonance imaging (fMRI) was used to gain more insight in the mechanism underlying a decline in recognition memory function with age. Twelve young (23–27 years) and 12 older (63–67 years) healthy men performed two types of word encoding tasks, in which words were either incidentally or intentionally encoded for storage in memory. After a 30 min delay, participants performed a recognition task. Older participants were less accurate and slower than young on the recognition task. In the both groups, successful retrieval was accompanied by activation in the left inferior frontal gyrus, left precentral gyrus and right cerebellum. Older participants showed additional activity in the bilateral medial prefrontal gyrus and right parahippocampal gyrus. Correlational analyses showed that only the additional parahippocampal activation correlated positively with task performance in the older but not young participants, suggesting that activation in this area served the purpose of functional compensation. The additional activation in the medial prefrontal cortex, on the other hand, was explained in terms of increased conflict, that is, reduced distinction between target and distracter words leading to increased simultaneous activity of both response tendencies. In a comparison between incidentally and intentionally remembered words the young group showed additional activation in the right middle occipital gyrus. This last result was explained in terms of strategic differences between the young and older group.

© 2006 Elsevier Ltd. All rights reserved.

Keywords: Compensation, HAROLD; Neuroimaging; Memory; Conflict

1. Introduction

Normal healthy aging is accompanied by certain memory deficits. Older adults show these deficits on a broad range of memory tasks, but not all memory domains are equally affected by age. Retrieval is found to be more impaired than encoding (e.g. Craik & Jennings, 1992; Jolles, 1986; Smith, 1996), and especially recollection, as can be measured in recall tasks, deteriorates, whereas familiarity, as can be measured in recognition tasks, is relatively spared (e.g. Burke & Light, 1981). Furthermore, older adults perform less accurately on tasks with a relatively low level of contextual cues, which can help them in retrieving the memorized material. Behaviorally, it has been shown that priming is relatively spared in aging (see Fleschman & Gabrieli, 1998, for a review). In addition, in a recent functional Magnetic Resonance Imaging (fMRI) study, Lustig and Buckner (2004) found that the neural correlates of priming are also largely unaffected by effects of aging. This implies that the more or less automatic, externally driven memory processes might be generally unaffected by age. Self-directed and controlled memory processes, on the other hand, are strongly affected by age, as has been found in numerous studies (Craik & Jennings, 1992; Smith, 1996).

With the development of neuroimaging techniques it has become possible to examine the underlying brain mechanisms of these memory deficits. First, these techniques can be used to examine structural changes accompanying the normal aging process. By using structural MRI, it has become clear that the normal aging process leads to an overall decrease in brain volume (e.g. Raz et al., 1997; Tisserand, Visser, Van Bostel, & Jolles, 2000; Tisserand et al., 2004) and a loss in connectivity between functionally linked brain structures (e.g. Raz, 2000).
This loss in volume and connectivity is especially strong in the prefrontal cortex (PFC; Raz, 1997; Tisserand et al., 2000, 2004) and areas in the medial temporal lobe, such as the hippocampus and the parahippocampal gyrus (e.g., Tisserand et al., 2002, 2004). Evidence from functional neuroimaging (e.g., functional MRIs) regarding the presence or absence of age-related changes, however, is somewhat less consistent. It is often found that, to perform memory tasks, older participants activate additional brain areas compared to young, especially in prefrontal regions (e.g., Dalelaar, Voitman, Rombouts, Rasijmakers, & Jonker, 2003; Madden, Turkington et al., 1999). This finding has been explained in terms of functional compensation for deteriorating performance. A more specific finding in aging studies is contralateral PFC recruitment (see Cabeza, 2002, for a review). Healthy young adults mostly show lateralized activation in the PFC in both the encoding and retrieval phase of memory tasks. In the encoding phase, prefrontal activation is mostly lateralized to the left, whereas in the retrieval phase prefrontal activation is lateralized to the right. This pattern of brain activation is known as hemispheric encoding/retrieval asymmetry (HERA) (Cabeza, 2002). A more specific finding in aging studies is contralateral prefrontal cortex recruitment (see Cabeza, 2002, for a review). This contralateral prefrontal cortex recruitment has been explained in at least two different ways. According to the first view, as mentioned before, this additional activation can be seen as functional compensation. An alternative explanation can be found in the functional de-differentiation view (e.g., Cabeza, Anderson, Locantore, & McIntosh, 2002; Li, Lindenberger, & Slikstrom, 2001), in which it is stated that the age-related changes in brain activation reflect a more general deficit in brain functioning. According to this view, the additional activation in the elderly can be interpreted in terms of a more general spread of activation, which is caused by a reduction in functional specialization. In this way, the additional activation can either be or not be compensatory.

In order to interpret brain activation data it is important to relate the activation to performance. This can be done by computing correlations between performance measures and brain activation. Only if additional activation in memory tasks is accompanied by better task performance, can this activation be explained in terms of functional compensation. If no or even negative correlations are found, an increase in activation is apparently not beneficial to task performance. Negative correlations can, however, also point in the direction of functionally important decreases in activation. For instance, a decrease in activation in an area that interferes with the task at hand can be beneficial to task performance. These decreases in activation, however, are most likely not directly linked to the primary task and probably linked to a more general network of areas that routinely deactivates when an attention demanding task has to be performed.

Previous studies have reported mixed results with respect to the effects of aging on correlations between performance and brain activation. Several studies have reported positive correlations between memory performance and a number of prefrontal areas that were additionally activated by elderly (Gron et al., 2003; Grady, McIntosh, & Craik, 2005; Madden, Gmthob et al., 1999; McIntosh et al., 1999). On the hand, negative correlations have been reported for a number of other areas, such as the cuneus, transverse temporal cortex, posterior cingulate cortex, inferior parietal lobule, precuneus, precentral gyrus, parahippocampal gyrus and the pulvinar (Madden, Gmthob et al., 1999). Both positive and negative correlations have also been reported for several areas that were activated by both young and elderly participants (Lustig & Buckner, 2004). Together, these findings seem to support the view that prefrontal areas are used to compensate for deteriorating performance whereas additional activation in several other areas can be interpreted as dysfunctional, and not related to optimal task performance.

The present study examined the effect of aging on brain activation associated with a verbal episodic memory task and specifically focused on examining activation-performance associations to avoid problems associated with equating performance levels between age groups. A group consisting of younger participants aged around 25 years old was compared to a group of older participants aged around 65 years old. This study focused on the effects of aging on recognition of incidentally and intentionally stored words. The spontaneous use of encoding strategies declines with increasing age (Craik & Jennings, 1992), but this effect can be diminished by providing external cues (Park, Smith, Morrel, Pugliani, & Dudley, 1999). Besides the expectation that elderly participants would respond slower and less accurately in the recognition task, it was therefore expected that elderly participants would perform even less accurately on the incidental task in which no external cues are given. Previous studies have found either no effect of the type of encoding task (e.g., incidental versus intentional) on brain activation in the recognition phase (e.g., Bernstein, Beig, Siegenthaler, & Grady, 2002; Grady, McIntosh, Beig, & Craik, 2001), or found a trend towards a stronger electro-cortical response with an unchanged scalp distribution to correctly recognized intentionally encoded words (Van Hoof, 2005). Therefore, it was hypothesized that recognition of intentionally stored words would activate the same brain areas as recognition of incidentally stored words, but that the activation of these areas would possibly be somewhat stronger.

Participants first performed an intentional and incidental word encoding task, after which they performed a recognition task. It was hypothesized that the correct recognition of previously presented words as compared to the correct rejection of new words would be accompanied by activation in the inferior and superior parietal cortex, medial parietal cortex, posterior cingulate cortex, bilateral anterior PFC, right dorsolateral PFC and left ventrolateral PFC in both age groups (for a review see Rugg & Henson, 2002). Furthermore, it was expected that older participants would activate additional brain areas, especially contralateral prefrontal cortex areas, to perform the same recognition task. It was expected that the recruitment of additional brain areas would be stronger in the incidental condition, which was the condition in which the largest effects of aging on performance were expected. Finally, we explored whether such additional activation was related to the participants’ performance. Additional activation, which correlates positively with performance...
measures should provide more support to the functional compen-
sation view, whereas no correlation or even negative correlations
would provide more evidence for the de-differentiation view.

2. Methods

2.1. Participants

Twenty-four right-handed males participated in this study. Despite the rig-
sorous screening (see below), several participants were excluded at some point in
the experiment. Two participants could not perform the cognitive task, one experi-
enced claustrophobia during the scan session and one participant had
hypertension. These participants were subsequently replaced by other ones.
Twelve young participants between the age of 23 and 27 (mean 25.1) and 12
elderly participants between the age of 63 and 67 (mean 64.7) were included.
The age of 65 years was chosen in order to reduce the possible influence of age-
related factors, such as subclinical health problems, subtle mood changes and
psychosocial factors (Houx, Vreeling, & Jolles, 1992; Jolles, Verhey, Reidell, &
Houx, 1995; Van Boxtel et al., 1998). Care was taken to reduce the effect of these
possible confounders as much as possible. This was done in the present study by
the use of a group of young-adult participants who had also received a good medical
screening. The present study, by using somewhat younger elderly participants
than used in most other studies, gives a conservative estimation and yet provides
clear effects of the factor age. All participants were matched for educational level
(education 3–6 on a 7 point scale; CBS, see Jolles et al., 1995). Care was taken to
reduce the effect of the number of items, which referred to living versus non-living.

2.2. Task design

Participants performed a verbal episodic memory task consisting of an
encoding and retrieval phase, both presented in the MRI scanner. Only the
imaging data of the retrieval phase will be described in the current paper. In the encoding phase, mono-syllabic or bi-syllabic Dutch words, varying in length
between five and seven letters, were projected on a semi-transparent screen.
These words were presented in blocks consisting of 16 words each, and words
were presented for 1 s with an inter-stimulus interval of 2 s. A total of 24 blocks
were presented, divided over two separate sessions. Before the start of every sin-
gle block the participants received a verbal instruction on the screen, instructing
them to perform one out of four possible tasks. In the first task, participants were
asked to make a decision about the use of the letters, upper-case or lower-case, in
the second task they had to decide whether or not the word contained the letter ‘e’, as the third task they had to decide whether the word represented something
living or non-living, the fourth task was the same as the third, but the partic-
ipants were also asked to memorize the word. Every task was repeated three
times with the same instruction and the same words, so each session consisted of
three repetitions of all four tasks. Task blocks were mixed in a pseudo ran-
dom way. Three clusters of task blocks consisting of one instance of each task
were created. Within these clusters, the order of the tasks was varied randomly
and these clusters were presented in a random order. Concrete words that are
acquired early in life were used, and were matched for word frequency, word
length and categories of words (e.g. number of animals, furniture, parts of the
human body). Each task block consisted of eight uppercase and eight lowercase
words. Also, eight words contained the letter ‘e’ and eight words did not, and
the same applied to the number of items, which referred to living versus non-living.
The encoding sessions were counterbalanced across all four encoding conditions
with only the task instructions differing. The words that were used in the practice session (see below) were not used in the scan session. Participants responded with either their left or right index finger using two response devices. Pressing the right button
always indicated ‘yes’, pressing the left button always indicated ‘no’. Directly
after the end of a session of the 12 task blocks participants were asked to recall
the words from the memorizing condition. Total time for both sessions in the
encoding phase was about 20 min. Data of the encoding phase are presented
elsewhere (Houx, Mcintosh, van der Veen, Backer, & Jolles, 2005).

In the retrieval phase, a total of 104 words were projected on a screen. Words were selected from three categories. The first category consisted of 26 words
that were randomly selected words from the 32 words presented in the encoding
condition that were asked to be memorized (intentionally encoded). The second
category consisted of 26 words that were randomly selected from the 32 words
presented in the living/non-living encoding condition, which were not explicitly
asked to be memorized (incidentally encoded). The third category consisted of
52 new words. All categories were randomly mixed. The task consisted of two
sessions consisting of 52 stimuli each. Participants were asked whether they
saw the word before or not. The retrieval task started with the instruction on the
screen for 5 s, followed by a black screen for 5.5 s. Each stimulus was presented
for 2 s and the inter-stimulus interval was 12.25 s. The task was completed by a
black screen that was presented for 5.5 s. Participants responded again by using
the same response devices that were used for the encoding task. Total time for
both sessions in the recognition phase was about 22 min.

2.3. Procedure

The complete experiment consisted of two sessions. The first session was the
practice session and the second session was the scan session that took place approxi-
mately 1 week later. In the first session, the participants were instructed
and practiced the encoding task on a laptop. After verbal instruction, the par-
ticipants performed 12 blocks consisting of 16 stimuli each of the 4 different encoding
tasks. This means that they practiced every task twice. Instead of the words used in the practice session were used in the scan session. The
encoding task was not practiced, and participants were only asked to recall
the words from the intentional encoding condition. The tasks were practiced
while listening to background noise recorded from the scanner to simulate the
noisy scanner environment. Before the start of the scan session, participants
were instructed for a second time. During this session, participants viewed the
stimuli through a mirror that was attached to the head coil, on a semi-transparent
screen positioned approximately 100 cm from the bore of the magnet. Partici-
pants first performed two runs of the encoding task followed by two runs of the
recognition task. Imaging was performed on a 1.5 T Philips ACS-NT scanner
(Philips Medical Systems, Best, The Netherlands). Readout motion was minimized
by using two foam cushions and a tape across the participant’s forehead. The
functional scan session consisted of a single shot multiple slice T2* sensitive
echo-planar imaging (EPI) sequence, sensitive to the Blood Oxygenation-Level-
Dependent (BOLD) contrast. Parameters were TR 3.5 s, TE 40 ms, flip angle
90°, matrix dimension 64 × 64, 36 contiguous slices and an isotropic voxel size
of 3.5 mm3. Before the acquisition of the functional images, two dummy full
brain scans were acquired to run the system into a stable stationary mode. For
anatomical reference, a 3D T1 weighted fast-field echo scan was acquired with
parameters TR 11 ms, TE 5.5 ms, flip angle 90°, matrix dimensions 256 × 256, 150
continuous slices and an isotropic voxel size of 1 mm3.

2.4. Image processing

Before performing the statistical analysis, all images were preprocessed
using the SPM99 software (Wellcome Department of Cognitive Neurology,
London, UK), implemented in Matlab (Mathworks, Natick, MA, USA). All
participants’ images were first corrected for slice acquisition time, and were
subsequently realigned to the mean image (head movement was less than 3 mm
in all cases) and resliced using sinc interpolation. In the next step, images were
spatially transformed, by bilinear interpolation, to a standard EPI template using
12 non-linear basis functions (with resulting voxel sizes of 2 mm3), and spatially
smoothed with an 8 mm full-width half maximum Gaussian filter.

2.5. Statistical analysis

Performance measures (percentage correct and response time) were statisti-
cally evaluated with a mixed factors analysis of variance (ANOVA) with stimulus
category (three levels, correctly recognized intentionally remembered words, correctly recognized incidentally remembered words and correctly rejected distractor words) as within-subjects factor and age group (two levels, old versus young) as between-subjects factor. Where appropriate, the statistical degrees of freedom were adjusted using the Greenhouse-Geisser correction.

With regards to the analysis of the MRi data, an event-related approach was used. Each event was modeled using a delta function convolved with the canonical hemodynamic response function and was modeled to the onset of a stimulus event. Four different stimulus event types within the two sessions were modeled separately: correctly recognized target words from the intentional condition, correctly rejected distractor words and erroneous responses were modeled separately. For all participants, individual activation maps were created. Two different contrasts were created to examine task-related brain activation. First, the difference between correctly recognized target words (intentional + incidental), CorRec) and correctly rejected distractor words (CorRej) items was computed, to examine the brain areas involved in successful retrieval of previously acquired verbal information. Second, the difference between correctly recognized items from the incidental and intentional categories were compared to examine possible differences in retrieval strategy for intentionally and incidentally memorized words. A random-effects approach was used, in which the individual contrast images were further analyzed in a second level analysis to examine whether individual brain activation patterns were consistent over participants (one-sample t-test) and whether groups of participants differed in their activation patterns (two-sample t-test). If the two-sample t-tests analyses yielded significant interaction effects, follow-up analyses were performed by computing mean signal change in the significant cluster separately for all conditions and groups, using the MarsBar tool (Brett, Arton, Valabregue & Poline, 2002). A final analysis was performed on the contrast images of CorRec–CorRej, in which correlations between brain activation and percentage correctly recognized items were computed. For all statistical images, a significance level of p < 0.01 (uncorrected) was used, and an extent threshold of 10 voxels. For the whole brain analysis, clusters significant at p < 0.05 corrected (family-wise error), and clusters containing a peak voxel significant at p < 0.05 corrected, are reported as significant areas of activation. From previous studies (Cabeza et al., 2004; Rugg & Henson, 2002), specific a priori predictions concerning activated areas in similar recognition tasks could be derived. Based on these predictions we defined a number of regions of interest (ROIs) which were extracted from the Automated Anatomical Labeling (AAL) map based on the MNI average brain (Tzourio-Mazoyer et al., 2002). Brain activation changes in these ROIs were analyzed by using the small volume correction (SVC) approach in SPM (thresholded at p < 0.05, corrected). Due to the difference in the hand used by participants for indicating a previously presented word or a new word, it was expected that lateralized primary motor cortex would be present when comparing brain activation accompanying previously presented and new words. Therefore, additional ROI analyses were performed for the left and right precentral gyrus (BA4). Furthermore, based on earlier work in which correctly recognized words were compared to correctly rejected words (see Rugg & Henson, 2002, for a review) ROI analyses were performed in the inferior and superior parietal cortex (Brodman area BA 7, 39, 40), middle parietal cortex (BA 7), posterior cingulate cortex (BA 23, 31), bilateral anterior PFC (BA 10), right dorsolateral PFC (BA 9, 46) and left ventromedial PFC (BA 45, 47). Finally, ROIs were defined in the parahippocampal gyrus and hippocampus based on the recently reported finding that the young and elderly differentially activate hippocampal and parahippocampal areas in an episodic retrieval task (Cabeza et al., 2004). Follow-up analyses were performed for significant group by task interactions using the MarsBar tool (Brett et al., 2002). This was done by computing the mean response strength separately for the three age groups and the interaction effects for the cluster where the significant interaction was found.

3. Results

3.1. Performance

Speed and accuracy measures of recognition performance are presented in Fig. 1. The percentage correctly recognized words and the response times (RT) were tested separately in a design with stimulus category and age group as factors. For RT, only a main effect of group, F(1,22) = 8.2, p < 0.01, was found. As expected, the elderly participants responded slower than the young participants. For accuracy, this analysis revealed effects of age group, F(1,22) = 17.5, p < 0.001, and stimulus category, F(1,44) = 20.5, p < 0.001, and a significant interaction between these two factors, F(2,44) = 6.6, p < 0.05. Post hoc tests, in which the three stimulus categories were examined separately, showed that the elderly participants recognized words from the intentional and incidental category less accurately than the young, whereas both groups were equally accurate at rejecting the distracter words. Additional follow-up analyses, in which the stimulus categories were directly compared, showed that in both groups words from the incidental condition were recognized less accurately than words from the intentional condition, and that new words were categorized more accurately than old words. In a more specific follow-up analysis, d-prime was calculated, which indicates the ability to discriminate between targets and distracter (Green & Swets, 1966). The elderly participants had a lower d-prime score (1.4 versus 2.0, t(22) = 2.5, p < 0.05), pointing in the direction of lower sensitivity in discriminating target from distracter items. Furthermore, the criterion measure beta was calculated, which indicates the minimum level of activation necessary for a participant to respond to a target (Green & Swets, 1966). Elderly and young participants did not differ with respect to this parameter, t < 1. Finally, we tested the pos-
A first question in this study was whether aging affects brain activation accompanying successful retrieval. In order to answer this question, we examined the contrast correctly recognized (CorRec) items minus correctly rejected distracter words (CorRej). Table 1 lists the brain areas that showed significant activation in this contrast. In the whole brain analysis for both age groups combined, significant activation was found in an area overlapping the left inferior frontal gyrus (BA 47) and the left superior temporal gyrus (BA 37). Furthermore, significant activation was found in the right cerebellum. In the analysis of the predefined ROIs, significant activation was found in the left inferior frontal gyrus (BA 47) and left precentral gyrus (BA 4).

In the opposite contrast, in which CorRej minus CorRec was computed, only one cluster was significantly activated. In the whole brain analysis in both groups combined, it was found that the right precentral gyrus (BA 4) was activated. The analysis of the predefined ROIs did not reveal any additional activated brain areas.

Interaction effects between age group and stimulus category were examined by computing two different contrasts, namely old (CorRec–CorRej)–young (CorRej–CorRec) and young (CorRec–CorRej)–old (CorRej–CorRec). Only in the old–young contrast significantly activated brain areas were found, which are shown in Fig. 2. In the whole brain analysis, it was found that one cluster in the right parahippocampal gyrus (BA 28) was significantly more activated in the old. Follow-up analyses, in which mean signal change was computed for the two age groups and the two stimulus conditions separately, showed that the elderly group activated the bilateral medial prefrontal gyrus and right parahippocampal gyrus in the CorRec condition, whereas the younger did not activate or even deactivated these areas. Results of these follow-up analyses are shown in Fig. 3.

### 3.2. Correlation accuracy and brain activation

A specific question in the present study was whether the additional brain activation found in the group of older partic-
Fig. 2. Enhanced brain activation in the elderly participants in the medial frontal gyrus (most significant voxel of this cluster is located at Talairach coordinates \(-12, 24, 56\)) and parahippocampal gyrus (most significant voxel of this cluster is located at Talairach coordinates \(22, -11, -23\)) in the contrast correctly recognized-correctly rejected.

Fig. 3. Mean activation scores as computed by MarsBar (Brett et al., 2002) in correctly recognized target items and correctly rejected distracter items for young and elderly participants, in the bilateral medial frontal gyrus (top panel) and two right parahippocampal areas (bottom panel). Talairach coordinates indicate the location of the most significant voxel in each cluster.

Table 2
Talairach (XYZ) coordinates and Z-scores of peak voxels of brain areas showing activation in the comparison between correctly recognized items from the incidental and intentional category

<table>
<thead>
<tr>
<th>Region of activation</th>
<th>Left/right</th>
<th>Brodmann area</th>
<th>Cluster size</th>
<th>Z-score</th>
<th>X</th>
<th>Y</th>
<th>Z</th>
</tr>
</thead>
<tbody>
<tr>
<td>Incidental-intentional (young &gt; old)</td>
<td>Left</td>
<td>18</td>
<td>190</td>
<td>4.64*</td>
<td>26</td>
<td>-89</td>
<td>8</td>
</tr>
</tbody>
</table>

* p < .05 corrected at cluster level, peak voxel significant at p < .05 corrected.
Fig. 4. Mean activation scores as computed by MarsBar (Brett et al., 2002) in correctly recognized target items in the intentional and incidental condition for young and elderly participants, in the right middle occipital gyrus. Talairach coordinates indicate the location of the most significant voxel in this cluster.

Participants was beneficial for task performance or not. Beneficial brain activity should lead to better performance (positive correlation between performance and brain activation), and would be suggestive of a compensatory mechanism. In order to answer this question, in the elderly group associations were examined between brain activation in the CorRec–CorRej contrast and the percentage correctly recognized items in a second-level analysis. Correlation with brain activation in the intentional–incidental contrast was not computed because no additional brain activation for the elderly was found in this contrast. The results of this analysis are presented in Table 3. For the whole brain analysis, this analysis revealed that brain activity in the left parahippocampal gyrus (BA 37) and the left lingual gyrus (BA 19) correlated positively with the accuracy measure. In the analysis of the predefined ROIs, additional significant clusters were found in the right and left parahippocampal gyrus (BA 37 and 28, respectively).

Negative correlations in the older group were also computed, and the results of this analysis are presented in Table 3. In the whole brain analysis, it was found that brain activation in the bilateral posterior cingulate gyrus (BA 24) and the bilateral inferior parietal gyrus (BA 40) negatively correlated with accuracy.

In order to compare the results reported above for the older group to the results of the younger group, similar correlation analyses were performed for the younger group. These analyses, however, did not reveal any significant effects.

4. Discussion

In the current study, the effects of aging on recognition in a verbal episodic memory task and the accompanying brain activation were examined. Older participants responded less accurately and slower than young. Furthermore, whereas young and older adults activated a number of similar brain regions during successful retrieval correctly recognized targets minus correctly rejected distractors), the older participants showed additional activation in parahippocampal and medial prefrontal areas when correctly recognized targets and correctly rejected distractors were compared, and reduced activation in the middle occipital gyrus when correctly recognized words from the intentional and incidental condition were compared.

Aging affected task performance in a more or less expected way. The slower reactions of the older participants were independent of the type of stimulus (target or distracter) that was presented, which is in accordance with a general finding in the cognitive aging literature that response speed declines with age (e.g. Salthouse, 1996). Furthermore, elderly participants were less accurate in recognizing target words, but as accurate in rejecting distracter words. Follow-up analyses using measures derived from signal detection theory (Green & Swets, 1966) showed that elderly participants were less sensitive in discriminating target from distracter words without changing their criterion. This can be either due to a weaker signal (weaker memory trace) or more noise (more interfering processes). These possibilities cannot be distinguished by using these performance measures.

Aging did not differentially affect recognition of incidental and intentionally memorized words, in line with a previous study (Tellez-Alanis & Cansino, 2004), but in contrast with another

Table 3

<table>
<thead>
<tr>
<th>Region of activation</th>
<th>Left/right</th>
<th>Brodmann area</th>
<th>Cluster size</th>
<th>Z-score</th>
<th>X</th>
<th>Y</th>
<th>Z</th>
</tr>
</thead>
<tbody>
<tr>
<td>Positive correlation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parahippocampal gyrus</td>
<td>L</td>
<td>37</td>
<td>243</td>
<td>4.64</td>
<td>−32</td>
<td>−49</td>
<td>−1</td>
</tr>
<tr>
<td>Lingual gyrus</td>
<td>L</td>
<td>19</td>
<td>227</td>
<td>4.29</td>
<td>−12</td>
<td>−64</td>
<td>7</td>
</tr>
<tr>
<td>Parahippocampal gyrus</td>
<td>L</td>
<td>37</td>
<td>14</td>
<td>4.50</td>
<td>−34</td>
<td>−45</td>
<td>−1</td>
</tr>
<tr>
<td>Parahippocampal gyrus</td>
<td>R</td>
<td>28</td>
<td>52</td>
<td>4.17</td>
<td>30</td>
<td>−18</td>
<td>−19</td>
</tr>
<tr>
<td>Negative correlation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inferior parietal gyrus</td>
<td>R</td>
<td>40</td>
<td>18</td>
<td>5.18</td>
<td>57</td>
<td>−32</td>
<td>26</td>
</tr>
<tr>
<td>Posterior cingulate gyrus</td>
<td>L</td>
<td>24</td>
<td>238</td>
<td>6.53</td>
<td>−12</td>
<td>−10</td>
<td>39</td>
</tr>
<tr>
<td>Posterior cingulate gyrus</td>
<td>R</td>
<td>24</td>
<td>584</td>
<td>4.51</td>
<td>12</td>
<td>−18</td>
<td>36</td>
</tr>
<tr>
<td>Inferior parietal gyrus</td>
<td>L</td>
<td>40</td>
<td>246</td>
<td>3.84</td>
<td>−50</td>
<td>−45</td>
<td>37</td>
</tr>
</tbody>
</table>

* Significant in ROI analysis.
* p > .05 corrected at cluster level, peak voxel significant at p < .05 corrected.
eral medial prefrontal gyrus than the young. This finding is in accordance with these findings is the recent suggestion of Lepage (2004), and has been associated with post-retrieval monitoring (recollect) and items that are merely known (familiar). Recent event-related fMRI studies (Henson, Rugg, Shallice, & Dolan, 2000; Henson, Rugg, Shallice, Josephs, & Dolan, 1999) have shown similar left lateralized activation in the prefrontal cortex when the participants both know and remember learned items, and give a high confidence rating for the remembered test item. This suggests that both the young and older participants in this study might have used a relatively conservative response strategy, and only indicated that they saw the word before when they were certain that they saw it before (i.e. recollect). In line with these findings is the recent suggestion of Lepage (2004) that left lateral prefrontal cortex is involved in retrieval success and right prefrontal areas are more strongly involved in memory search and monitoring (retrieval attempt). This suggestion is based on findings in a PET study in which high cued-recall was associated with left lateral prefrontal activation and low cued-recall with right prefrontal activation. Finally, activation in the right cerebellum has also been reported in previous studies, and has been associated with initiation of action (Cabeza et al., 1997, 2004) coordination and integration of recognition memory processes (Kim et al., 1999) and learning processes (Poldrack & Gabrieli, 2001).

The older participants showed stronger activation in the bilateral medial prefrontal gyrus than the young. This finding is in accordance with findings of Grön et al. (2003), who reported age-related additional activation in this area during recall of abstract geometric patterns. A number of recent studies have related activation in the medial wall of the prefrontal cortex to response conflict (e.g. Carter et al., 1998; Kerns et al., 2004). An explanation in terms of response conflict fits our data. As stated above, it seems that older participants were less sensitive in discriminating target and distractor words. This means that the distributions of both stimulus categories have stronger overlap, and in this way the two response tendencies are more frequently activated at the same time. This leads to stronger conflict, and therefore the additional activation in the medial prefrontal cortex might well be a reflection of this. Additionally, an explanation in terms of more effort might also fit our data. However, activation in the medial prefrontal area did not correlate with accuracy, indicating that stronger activation in this area was not accompanied by more accurate decisions.

Stronger activation in the right parahippocampal gyrus during successful retrieval in the older participants is in accordance with recent findings of Cabeza et al. (2004), who reported additional activation in the left parahippocampal gyrus in a comparable recognition task. These authors also reported a decrease in hippocampal activation, which was not found in the present study. They argued that their findings are in line with the suggested differential vulnerability of recollection-based versus familiarity-based memory to the effects of aging. The hippocampus is thought to be involved in recollection, whereas the parahippocampal gyrus is thought to be involved in familiarity (e.g. Aggleton & Brown, 1999). In the present study, which used a familiarity-based recognition task, we did not find support for the sparing of familiarity-based memory processes with aging. Performance in the recognition task, however, was related to the activation of the right parahippocampal gyrus in the older group, as was shown in the correlation analysis. More accurate performance was accompanied by stronger activation in this area, and therefore it can be interpreted in terms of functional compensation.

The finding of reduced activation in the middle occipital gyrus in the older group when successfully recognized targets from the intentional and the incidental condition were compared was unexpected and no specific hypotheses considering this area were formulated. Previous studies have reported a generalized task-independent reduction of activation in occipital areas in the elderly (see Cabeza, 2001, for a review). This finding has been interpreted in terms of less efficient processing in the ventral visual processing stream. However, as can be seen in Fig. 4, the effect in the present study was due to reduced activation in the incidentally stored items and not in the intentionally stored items. Therefore, it is unlikely that a general process like less efficient processing is responsible for this effect. The data suggest enhanced visual processing of the incidentally stored items for the young participants, and therefore it could be speculated that this specific effect is due to subtle strategic differences. Young participants might have relied on enhanced visual processing to recognize the incidentally stored words, whereas older participants relied on other types of processing.
The finding that activation in the bilateral posterior cingulate gyrus and bilateral anterior parietal gyrus correlated negatively with accuracy in the older group is in accordance with the study of Madden, Gottlieb et al. (1999), who reported similar negative correlations with a reaction time measure that was specific to the older group. As was suggested by these authors, these findings can possibly be interpreted in terms of decreased brain activation caused by reduced sensory processing of the target words. Target words were presented before, in the encoding phase, and therefore needed less sensory processing, which led to decreased activation in the target minus distractor contrast. In this way, performance correlates negatively with brain activation. It is unclear, however, why this effect is specific to the older group. There is evidence that the performance of older people and subjects with mild mood problems on information processing tasks is characterized by increasing slowness (e.g. Brand & Jolles, 1987; Den Hartog, Derix, van Bemmel, Kremer, & Jolles, 2003; Van Heeren et al., in press). Mild mood problems are rather common in otherwise healthy older people (e.g. Vinkers et al., 2005). They may be able to perform the task but they have to invest more effort and rely more on a controlled processing strategy. Conversely, young subjects perform tasks more according to automatic processing; they recruit less cortical regions in order to perform the task. This may underlie the lack of correlation between task performance and brain activation in the younger group.

To conclude, the present study found evidence supporting functional compensation in the elderly. It did not find evidence in support of contralateral prefrontal cortex recruitment, as reported previously (Cabeza et al., 2002, 2004). Correlational analyses showed that not all additional activation in the elderly should be interpreted in terms of functional compensation. Additional activation that does not correlate or correlates negatively with performance is apparently not contributing to better task performance, and therefore there are no clear indications for a functional role of this activation. Finally, it should be noted that performance, and therefore there are no clear indications for a functional role of this activation. Finally, it should be noted that performance is apparently not contributing to better task performance and brain activation in the younger group.

References


M154.

