

Age effects on brain activity associated with episodic memory retrieval

An electrophysiological study

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Summary

Electrophysiological correlates of episodic memory retrieval (recollection) were investigated in a young (18–30 years) and an older group (62–79 years) of healthy subjects ($n = 16$ per group). At study, subjects listened to words spoken in either a male or a female voice, and were instructed to perform one of two tasks depending on the voice in which the item was spoken. At test, subjects made initial old/new judgements to visually presented words and, for words judged old, either indicated in which voice they had heard the word at study (source task), or whether they ‘remembered’ or ‘knew’ they had heard the word at study (‘remember/know’ task). The accuracy of the initial recognition decision did not differ between the two groups. However, young

subjects were significantly more accurate in their source judgements than the older group. The magnitudes and topographical distributions of differences between event-related potentials to successfully recollected words and new words were indistinguishable for the two tasks. These event-related potential effects were also equivalent in magnitude and scalp topography in the two age groups, the only difference between the groups being a relative delay in the onset of the effects at some electrode sites in the older subjects. These findings are consistent with the proposal that the processes supporting episodic retrieval, including those dependent upon the prefrontal cortex, are relatively unaffected by advancing age.

Keywords: ageing; episodic memory; frontal cortex; recollection; source memory

Abbreviations: ERP = event-related potential; MMS = Mini-Mental State Test; NART = National Adult Reading Test; WMS-R = Wechsler Memory Scale—Revised

Introduction

The ability to remember recently experienced events declines with advancing age (Light, 1991; Craik and Jennings, 1992). Performance does not, however, decline uniformly across different kinds of memory test. On many indirect tests, designed to tap implicit memory for recent experiences, performance remains largely unchanged with age (Light and Lavoie, 1993). And on direct tests, intended to tap explicit memory, the effects of age differ according to the type of test. Age differences in recognition memory are generally found to be smaller than age differences on tasks such as free recall (Craik and Jennings, 1992). Age-related memory impairments are particularly evident on tests of source memory, studies of which have generally found greater age effects on memory for the context in which an item was experienced than for the item itself (Spencer and Raz, 1995).

The finding that age-related differences in memory performance are large when information must be both retrieved and placed in its appropriate spatiotemporal context

is consistent with the idea that episodic memory—the recollection of specific past events (Tulving, 1983)—is especially vulnerable to advancing age. This idea receives additional support from studies employing the ‘process dissociation’ (Jacoby, 1991) and ‘remember/know’ (Tulving, 1985) procedures. The findings from these studies (Fell, 1992; Parkin and Walter, 1992; Jennings and Jacoby, 1993; Perfect *et al.*, 1995) suggest that the detrimental effects of age are limited to conscious recollection, with a relative sparing of ‘familiarity’, a form of memory held to be independent of that supporting recollection (Mandler, 1980; Jacoby and Kelley, 1992).

Indirect evidence suggests that the age-related decline in episodic memory is related to changes in the functional integrity of the prefrontal cortex. This evidence comes from reports that the performance of older subjects on tests of memory for source (Craik *et al.*, 1990) and recency (Fabiani and Friedman, 1997), as well as the probability of endorsing

a recognized word as 'remembered' in the 'remember/know' procedure (Parkin and Walter, 1992; but see Perfect *et al.*, 1995), all correlate with performance on the Wisconsin Card Sorting Test (WCST), a test sensitive to damage to the dorsolateral prefrontal cortex (Milner, 1963). Together with evidence that focal damage to prefrontal cortex impairs source and recency memory (Stuss *et al.*, 1994), and that this region is strongly affected by age-related neuronal loss (Haug and Eggers, 1991), these correlations have led to the proposal that a decline in the functional integrity of the prefrontal cortex is an important cause of age-related changes in memory function (e.g. see West, 1996).

More direct evidence for age-related differences in brain function during memory retrieval has been sought using PET. The findings from these studies (Grady *et al.*, 1995; Schacter *et al.*, 1996; Backman *et al.*, 1997; Cabeza *et al.*, 1997) provide a rather inconsistent picture, notably with respect to the question of whether there are age differences in the engagement of the prefrontal cortex during memory retrieval. Undoubtedly, these inconsistencies are, to a large extent, attributable to the many procedural differences between the studies. There are, however, two problems, shared by all of the studies, which may have contributed to the variability of their findings, and which in any case constrain their interpretation.

The first problem arises because PET methodology does not permit brain activity to be sampled separately according to stimulus type or performance accuracy. Measures of brain activity obtained during memory tests are therefore integrated over trials on which retrieval is successful and unsuccessful. Evidence from neuroimaging (Rugg *et al.*, 1996b) and electrophysiological (Rugg, 1995; Wilding and Rugg, 1996) studies indicates that brain activity in several regions, including the prefrontal cortex, differs according to whether a test item elicits successful retrieval. When comparing retrieval-related activity across groups which differ in their performance, such as young and older subjects, it may therefore be difficult to distinguish age-related differences in retrieval-related brain activity from those that merely reflect the differential probability of successful retrieval in the two groups.

The second problem arises because performance on many common memory tests reflects the contributions of multiple forms of memory (Jacoby and Kelley, 1992). In particular, there is evidence to suggest that performance on standard tests of recognition memory (Jacoby, 1991) and cued recall (Toth *et al.*, 1994) receives a contribution from both episodic memory (recollection) and other, non-recollective, processes (familiarity, in the case of recognition, and implicit memory in the case of cued recall). As age-related effects are greater for episodic memory than for familiarity or implicit memory (Jennings and Jacoby, 1993; Light and LaVoie, 1993), it is possible for young and older subjects to show different patterns of brain activity during direct tests of memory not because episodic memory is supported by different brain structures, but because episodic memory makes less of a

contribution to performance in the older group. To overcome this problem, it is necessary to employ a retrieval task that permits test trials to be separated according to whether episodic recollection occurred, and a method of measuring brain activity that can be applied at the single trial level.

In the present study, brain activity associated with recollection was compared in young and older subjects using scalp-recorded event-related brain potentials (ERPs). The ERP method allows stimulus-locked brain activity to be averaged 'off-line', permitting measures to be obtained separately for studied and unstudied test items according to whether these items were correctly or incorrectly classified. It is therefore possible to investigate the stimulus-locked brain activity elicited specifically by test items that give rise to successful memory retrieval.

The starting point for the present study is a body of recent work suggesting that ERPs are sensitive to brain activity associated with the recollection of recently experienced events, where recollection is defined as the ability to identify the context in which a recognized test item was experienced. In a variety of test procedures, recollected items have been found to elicit ERPs which differ in a characteristic fashion from those elicited by unstudied items.

The left parietal 'old/new' effect consists of a positive-going wave, found in ERPs to recollected items, which is maximal at temporoparietal electrode sites and larger over the left than the right hemisphere; onset is ~400 ms post-stimulus and duration ~400–600 ms. The effect has been interpreted (Rugg *et al.*, 1996a) as a reflection of the contribution of the medial temporal lobe memory system to the retrieval of recently encoded episodes, possibly representing the hippocampally modulated cortical activity thought to underlie such retrieval operations (Alvarez and Squire, 1994; McClelland *et al.*, 1995).

In tasks requiring recognition to be accompanied by a source judgement (e.g. judging whether a test item was presented at study in a male or a female voice), a second ERP correlate of recollection has been described (Wilding and Rugg, 1996, 1997a, b; Rugg *et al.*, 1998).

Like the left parietal effect, the right frontal 'old/new' ERP effect has an onset at ~400 ms post-stimulus, but it is more sustained over time and is maximal over frontal regions of the scalp, where it exhibits a right-greater-than-left asymmetry. Again like the left parietal effect, the right frontal effect is larger when elicited by items that are correctly, rather than incorrectly, assigned to their encoding context, suggesting that it too reflects processes associated with the retrieval of memory for a specific prior episode (recollection). It has been suggested (Wilding and Rugg, 1996) that the right frontal effect reflects processes, supported by the prefrontal cortex, that operate upon the products of successful memory retrieval to generate the episodic memory representations necessary for judgements of source memory (Squire *et al.*, 1993; Knowlton and Squire, 1995).

In the present study the ERP correlates of recollection were investigated in young and older subjects using two

tasks that have been shown previously to give rise to left parietal and right frontal old/new effects: (i) a version of the source memory procedure described above; and (ii) an adaptation of the 'remember/know' procedure. The tasks were designed to give rise to relatively high levels of recollection (defined either as successful source memory, or the assignment of a recognized item to the 'remember' category), so as to permit a detailed analysis of the ERP correlates of successful recollection as a function of age. At issue is whether evidence can be found for age-related differences in the brain activity associated with recollection in measures of the scalp distribution, magnitude, or timing of the activity. Differences in scalp distribution would indicate that recollection engages different brain regions (or the same regions, but to differing degrees) in young and older subjects (Rugg and Coles, 1995). By contrast, differences limited to the magnitude or timing of memory-related effects would suggest that the same regions are engaged regardless of age, but with differing activation strengths or time-courses.

Method

Subjects

Seventeen young and 21 older subjects participated. The young subjects were drawn from the student population at the University of St Andrews, while the older subjects were recruited from an 'over 60s' exercise class consisting mainly of retired professionals. [The ERP and behavioural data from the young subjects are also reported in experiment 2 of Rugg *et al.* (1998).] The data from one young subject were rejected because task performance was too poor to permit the formation of ERPs from an acceptable number of trials. The data from five older subjects were rejected, four because task performance was too poor to permit the formation of ERPs and one because of technically unsatisfactory recordings. Of the 16 young and 16 older subjects whose data contributed to the study, all reported that they were in good health and that they were free from CNS-active medication. Each subject gave informed consent prior to participation in the study, which was approved by the Tayside Committee of Medical Ethics.

Neuropsychological tests

Subjects undertook several neuropsychological tests after they had completed the experiment proper. These included the National Adult Reading Test (NART; Nelson, 1982), selected subscales of the Wechsler Memory Scale—Revised (WMS-R) (Wechsler, 1987), and a measure of verbal fluency (letter- and category-cued word production). Older subjects were also administered the Mini-Mental State Test (MMS) (Folstein *et al.*, 1975). The results of these neuropsychological tests, and other characteristics of each group, are summarized in Table 1. As is evident from the table, young and older subjects were matched on the NART. Young subjects had

more years of full time education and outperformed the older subjects on verbal fluency, on WMS-R subscales of immediate and delayed logical memory, and on delayed visual reproduction.

Stimuli

Three hundred and twenty low frequency open class words (range, one to seven per million; Kucera and Francis, 1967), ranging in length from four to nine letters, were employed as the experimental stimuli. These words were used to form eight study lists, each containing 40 words. The ordering of the items in each of the study lists was randomly determined, and within each list half of the items were spoken by a single male voice and half were spoken by a single female voice.

The auditory stimuli were digitized at 22 kHz with 16-bit resolution. They were edited such that the beginning of the stored segment corresponded to the onset of the spoken word. The mean duration of these stimuli was 650 ms, and did not differ according to the gender of the voice. Each word was presented binaurally via headphones and the volume was adjusted, prior to the experiment proper, to a comfortable hearing level for each subject.

Four test lists were formed by randomly combining the items from a pair of study lists, and adding an additional four new items to act as fillers. Each of the test lists began with three of the filler items, the other filler occupying the first position after the rest point (see procedure below). The test items were presented in central vision (white on black) at a moderate contrast on a computer monitor. Each word was presented for a duration of 500 ms, and subtended a vertical angle of $\sim 0.5^\circ$, and a maximum horizontal angle of 2.8° .

Procedure

By combining each of the four test lists with one or other of its corresponding study lists, eight study-test blocks were created. These blocks were rotated across subjects so that each critical item appeared with equal frequency as a studied or an unstudied word in each of the two test tasks (source and 'remember/know').

Following electrode application (see below), subjects were seated in front of the stimulus presentation monitor, and the headphones positioned. Before the experiment proper each subject was presented auditorily with four words (two spoken in the female and two in the male voice) in order to adjust the volume to the subject's preferred level. These four words did not subsequently occur during the experiment. Subjects were informed that the aim of the experiment was to investigate memory for spoken words, and were given the instructions for the first task. Four study-test blocks, each containing a different set of items, were then administered. Approximately 5 min elapsed between the end of each study block and the commencement of the corresponding test task. During this interval, subjects were asked to count backwards

Table 1 Characteristics of the young and older groups

	Young (<i>n</i> = 16)	Older (<i>n</i> = 16)	<i>P</i> -value
Age (years)	22 ± 4	66 ± 6	
Handedness	16/16 right	16/16 right	
Sex distribution	9/16 female	13/16 female	
Education (years)	16 ± 2	13 ± 3	<0.01
WMS-R			
NART	126 ± 3	127 ± 4	n.s.
Verbal fluency	56 ± 7	47 ± 11	<0.005
Logical memory I	27 ± 5	21 ± 6	<0.01
Logical memory II	25 ± 5	16 ± 6	<0.0001
Visual reproduction I	35 ± 4	31 ± 5	n.s.
Visual reproduction II	35 ± 3	27 ± 7	<0.01
MMS	–	29 ± 1	

The MMS examination was administered to the older subjects only. Data are presented as mean ± standard deviation.

in steps of three from an arbitrary number, so as to block rehearsal of the study items. The time elapsing between the end of a test task and the next study task was also ~5 min.

Each study trial began with the presentation of a fixation point (an asterisk) for 1 s, which was erased 100 ms prior to stimulus presentation. Subjects were instructed to listen to each word and to respond verbally by repeating the word aloud, stating whether it had been presented in a male or female voice and, depending on the gender of the voice, either rating the word as 'pleasant/unpleasant' or as 'active/passive'. The voice in which each study item was presented therefore dictated which of two encoding tasks should be performed, a procedure first employed by Wilding and Rugg (1997*b*). The mapping of task to gender was counterbalanced across subjects. Stimulus presentation was paced by the experimenter, who also monitored the responses given on each trial.

For two of the test tasks subjects performed source judgements, and for the remaining two tasks they were asked to make a 'remember/know' discrimination. The two tasks were administered in an ABBA design, with half the subjects in each group starting with the source task, and half with the 'remember/know' task. The instructions for each test task were given immediately before it was first performed. Subjects who began with the 'remember/know' task were therefore unaware that they would subsequently have to perform source judgements on studied items.

For both test tasks, each trial began with the presentation of a fixation asterisk for 500 ms. This was erased 110 ms before the presentation of the test item. One second after the response to that item, a question mark appeared on the screen for 2.5 s to cue the second response. For both tasks, subjects were asked to judge whether each word was one that they had heard in the immediately preceding study task, or whether it was new, responding as quickly and accurately as possible by pressing a microswitch under the index finger of one or other hand. For each item that was judged old, subjects were required to wait until the question mark appeared, and then

to make a second judgement, again by pressing one of the two keys. In the source task, the requirement was to judge in which of the two encoding contexts the word had been presented at study, responding 'male' or 'female'. In the 'remember/know' task, subjects were instructed to decide whether they 'remembered' the old test word, or whether they simply 'knew' that it was old. The difference between these two forms of recognition was explained in the same terms as those employed previously (e.g. Gardiner and Java, 1991), and no reference was made to the fact that the studied item could be categorized by the gender of the voice in which it was heard at study. For each subject the same response key assignments were maintained across the four study-test blocks. These assignments were, however, counterbalanced across subjects in order to ensure that there were no correlations between the hands used for old/new, male/female, or 'remember/know' judgements. In addition to the specific instructions described above, subjects were also requested to maintain fixation, to stay relaxed, and to blink only when the fixation asterisk was displayed on the monitor. A brief rest break was given after the first 43 items of each test list.

ERP recording

ERPs were recorded from 25 scalp sites using tin electrodes embedded in an elasticated cap (Electro-Cap International, USA), sited according to the 10–20 system (Jasper, 1958) at three midline sites (Fz, Cz, Pz), the right mastoid process, and at 11 sites over each hemisphere; FP1/FP2, F7/F8, LF/RF (50% from the distance from F3 to F7 and F4 to F8), F3/F4, T3/T4, LT/RT (50% from the distance from C3 to T3 and C4 to T4), C3/C4, T5/T6, LP/RP (50% from the distance from P3 to T5 and P4 to T6), P3/P4, and O1/O2. EOG was recorded from a bipolar pair of electrodes placed on the outer canthus of the left eye and on the supra-orbital ridge of the right eye. All channels were referenced to the left mastoid, and ERPs were algebraically reconstructed off-line to represent

Table 2 Behavioural performance of each group

	Initial recognition		Judgement (correct source/remember)
	Correct rejection	Hit	
Accuracy			
Young group			
Source task	92.7 ± 6.7	85.2 ± 6.5	88.6 ± 6.3
Remember/know task	94.9 ± 6.4	83.8 ± 7.7	76.9 ± 8.9
Older group			
Source task	89.8 ± 8.5	80.5 ± 8.1	71.5 ± 10.0
Remember/know task	90.3 ± 7.8	84.2 ± 8.4	75.6 ± 14.1
Reaction times (ms)			
Young group			
Source task	1251 ± 292	1358 ± 335	1334 ± 323
Remember/know task	1310 ± 336	1284 ± 287	1207 ± 245
Older group			
Source task	1487 ± 343	1496 ± 343	1451 ± 317
Remember/know task	1543 ± 344	1307 ± 344	1221 ± 262

Accuracy = proportion of correct rejections and hits for the initial recognition decision, along with proportion of hits attracting correct source/remember judgements. Reaction times are for the initial recognition decision for each of the above response categories. Data are presented as mean ± standard deviation.

recordings with respect to a linked mastoid reference. EEG and EOG were filtered with a bandpass of 0.03–35 Hz (3 dB points), and sampled at a rate of 6 ms per point for an epoch of 1536 ms beginning 102 ms before test stimulus onset.

ERPs were formed for each subject for a variety of different response categories as described in the Results section. Trials on which base-to-peak EOG amplitude was >98 µV were rejected prior to averaging, as were trials on which baseline drift (the difference between the first and last data point) was >55 µV at any scalp site.

Results

Behavioural data

Accuracy and reaction-time measures are summarized for each group and task in Table 2. For the initial recognition decision, an ANOVA was conducted on the discrimination index 'phit-pfalse alarm', employing the factors of group and task. The main effect of group approached significance [$F(1,30) = 3.63, P < 0.07$] indicating a trend towards better performance on the part of the young subjects.

For both groups, source accuracy significantly exceeded the chance level of 50% [young group $t(15) = 23.27, P < 0.001$; older group $t(15) = 8.60, P < 0.001$]. Accuracy was, however, reliably greater for the young than the older subjects [$t(30) = 5.64, P < 0.001$]. The proportion of recognized items assigned a remember judgement did not differ between the groups.

The reaction times for responses to correctly classified new items, and for recognized old items that were assigned to their correct encoding context (source task), or to the remember category ('remember/know' task) were analysed by ANOVA, employing the factors of group, task, and response category (new versus old). This revealed main

effects for task [$F(1,30) = 7.63, P < 0.025$] and response category [$F(1,30) = 5.62, P < 0.025$], along with reliable interactions between group and response category [$F(1,30) = 4.43, P < 0.05$], and task and response category [$F(1,30) = 46.06, P < 0.0001$]. *Post hoc* Tukey tests indicated that the group × response category interaction arose because older subjects were slower to respond to new items than were the young subjects, but they responded with equivalent latencies to old items. Tukey tests also showed that the task × response category interaction arose because subjects were slower to respond to new than to old items in the 'remember/know' task, but not in the source task. In addition, responses to old items were faster in the former task.

ERPs

Analysis strategy

Prior to the analyses described below, preliminary analyses were conducted to determine whether the differences between ERPs elicited by new and 'recollected' items (i.e. recognized items attracting either a correct source judgement or a 'remember' response) differed according to task. These analyses were conducted on the data from each group separately, and took the form of ANOVAs (factors of task, response category—new versus recollected—and electrode site) of the mean amplitudes of consecutive 100-ms regions of the waveforms, extending from 300–400 to 1300–1400 ms post-stimulus onset. In neither group did these ANOVAs give rise to any effects involving the factor of task, and the same was true when the analyses were restricted to the data from those sites at which the ERP old/new effects were at their largest. In light of these findings, the waveforms for each subject were collapsed over the task variable for the purposes of further analysis. Thus, each subject's data was

reduced to two sets of ERPs, elicited by correctly classified new items, and 'recollected' old items, respectively. (Insufficient trials were available to form ERPs to items that were recognized but which either failed to attract a correct source judgement or were judged as 'known' rather than 'remembered'.) This had the effect of improving the signal-to-noise ratio of the ERP data and simplifying the across-group comparisons that constitute the analyses of central interest to the study. The mean number of trials contributing to the 'new' and 'recollected' categories were, respectively, 122 and 90 for the young group, and 98 and 68 for the older group.

The grand average ERPs elicited by new and recollected items are shown in Fig. 1A (young group) and Fig. 1B (older group). For both groups, the ERPs to recollected items are for the most part more positive-going than those elicited by new words. These old/new effects are widespread over the scalp, but show two distinct maxima, over left temporoparietal and right frontal regions of the scalp, respectively. The left parietal effect terminates before the end of the recording epoch, whereas the right frontal effect shows a more extended time-course.

The differences between ERPs to recollected and new items are represented more directly in Fig. 2, which shows the grand average subtraction waveforms (recollected minus new) for each group. The most striking difference between the old/new effects from each group is with respect to onset latency; other than over the lateral right frontal scalp, the effects appear to have an onset ~100 ms sooner in the young subjects. In addition, again with the exception of the right frontal scalp, the peak amplitudes of the effects appear to be somewhat greater in the young subjects.

The main analyses of these data were performed on the mean amplitudes of the same consecutive latency regions (i.e. 500–800, 800–1100 and 1100–1400 ms post-stimulus) that were employed in previous studies of the ERP correlates of recollection (e.g. Wilding and Rugg, 1996). These data, which are shown for selected electrode sites in Fig. 3, were subjected to three sets of analyses, as described below.

First, data from selected lateral electrodes were subjected to within-group ANOVAs, employing the factors of response category (new versus recollected), hemisphere (left versus right) and electrode site (LF/RF, LT/RT, LP/RP, T5/T6, O1/O1). The purpose of these analyses was to establish that the old/new effects were reliable for each group separately, and to allow a comparison with the findings from previous studies in which these sites had been selected for analysis.

Two sets of between-group comparisons were conducted. These were performed on the (recollected minus new) difference scores, so as to allow the old/new effects from each group to be compared directly. Group differences in the magnitude of the effects were investigated by ANOVAs of raw scores, while differences in scalp topography were investigated by ANOVA after the data had been rescaled to remove global differences in magnitude (McCarthy and Wood, 1985). These ANOVAs employed the factors of group

and electrode site. Subsidiary ANOVAs, restricted to data from subsets of electrode sites, were also conducted, and are reported when informative.

Within-group analyses

Young subjects. In all three latency regions, the ANOVAs gave rise to one or more significant effects involving the factor of response category.

For the 500–800-ms region there was a main effect of response category [$F(1,15) = 36.86, P < 0.001$], along with interactions between response category and hemisphere [$F(1,15) = 4.56, P = 0.05$] and response category and site [$F(1.5,22.7) = 4.93, P < 0.025$]; for the 800–1100-ms region there was a main effect of response category [$F(1,15) = 9.15, P < 0.01$]; and for the 1100–1400-ms region there was a reliable interaction between response category, hemisphere and electrode site [$F(2.0,29.3) = 5.31, P < 0.025$].

Older subjects. ANOVA of the 500–800-ms latency region revealed a main effect of response category [$F(1,15) = 46.04, P < 0.001$], and interactions between response category and site [$F(2.5,37.2) = 9.41, P < 0.001$], and between response category, hemisphere and site [$F(2.3,34.3) = 3.51, P < 0.05$].

The analysis of the 800–1100-ms region gave rise to an effect of response category [$F(1,15) = 5.05, P < 0.05$], and to a response category \times hemisphere \times site interaction [$F(1.9,28.1) = 7.09, P < 0.005$]. Similarly, ANOVA of the 1100–1400 ms epoch gave rise to a three-way response category \times hemisphere \times site interaction [$F(2.1,31.9) = 10.03, P < 0.001$].

In summary, the results of the within-subjects analyses indicate that in both groups, the ERPs elicited by new and recollected items differed reliably in each of the latency regions subjected to analysis.

Across-group analyses

Magnitude. For each latency region ANOVA revealed a main effect of site [for 500–800 ms, $F(5.2,155.8) = 5.98, P < 0.001$; for 800–1100 ms, $F(5.2,154.9) = 3.79, P < 0.005$; for 1100–1400 ms, $F(4.6,139.2) = 7.78, P < 0.001$], but no effect involving the factor of group [maximum F for main effect, $F(1,30) = 1.89$; maximum F for the group \times site interaction, $F(5.2,155.8) = 1.69$]. The site effects are elucidated in the topographic analyses described below.

Topography. The scalp topographies of the old/new effects are illustrated for each group and latency region in Fig. 4. ANOVA of the rescaled data revealed no evidence, in any latency region, of group differences in the scalp distribution of these effects [maximum F for the group \times site interaction, $F(5.4,161.7) = 1.57$].

The ANOVAs did, however, give rise in each case to highly reliable effects of site [for 500–800 ms, $F(5.4,161.7) =$

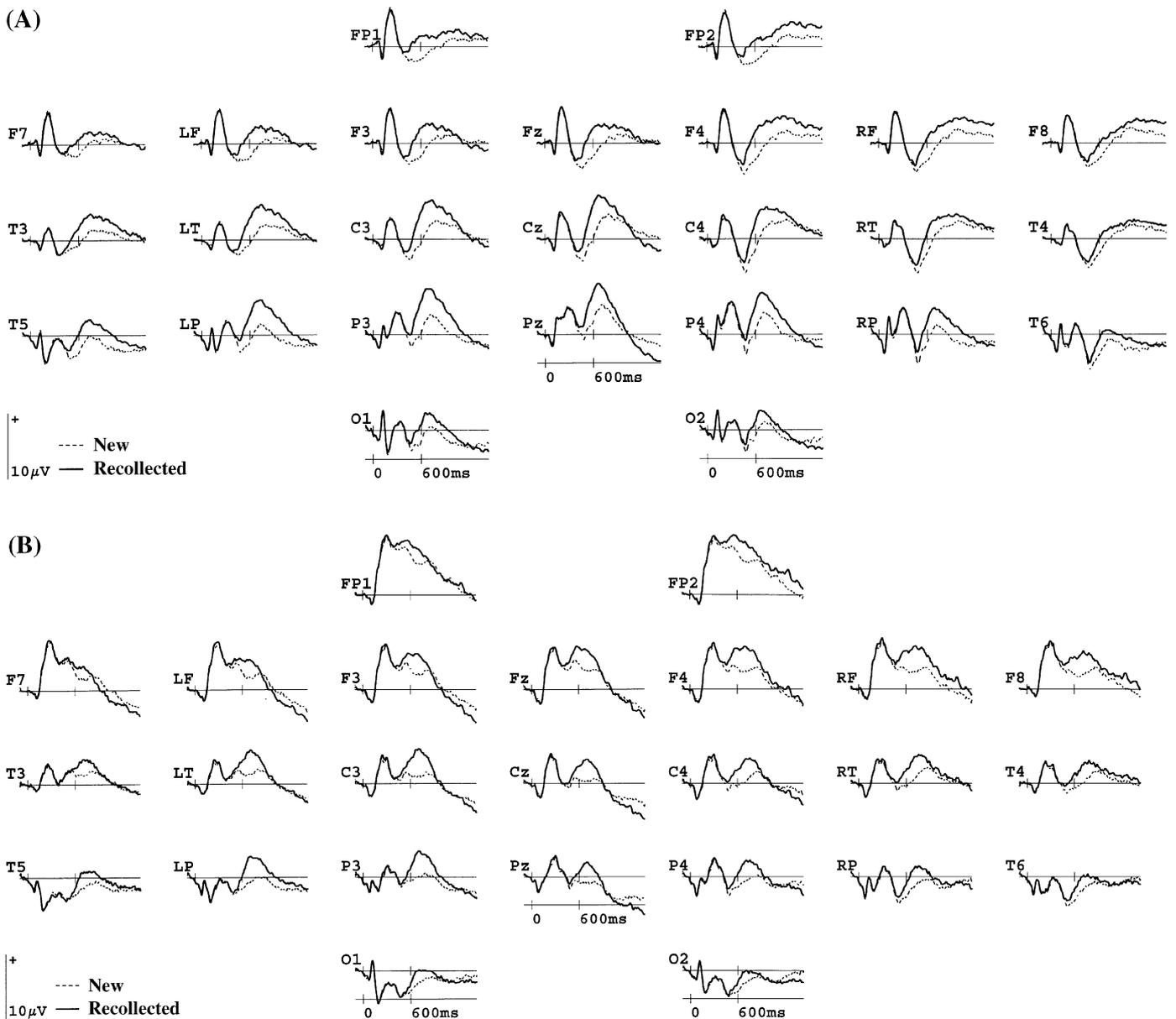


Fig. 1 Grand average waveforms for young (A) and older (B) subjects (collapsed across task) elicited by correctly judged new items (new = broken lines), and correctly judged old items that also received either an accurate source judgement or a remember response (recollected = unbroken lines). The electrode sites are laid out as if viewing the head from the top. The location of each site is described in the text.

5.89, $P < 0.001$; for 800–1100 ms, $F(5.1,151.7) = 3.68$, $P < 0.005$; for 1100–1400 ms, $F(4.7,140.7) = 7.79$, $P < 0.001$]. In light of these findings, subsidiary ANOVAs were conducted on the data from left and right lateral frontal (LF, RF) and parietal (LP, RP) electrodes, employing the factors of group, location (frontal versus parietal), and hemisphere. As before, no effect involving the factor of group approached significance. For each latency region, however, there was a significant interaction between location and hemisphere [for 500–800 ms, $F(1,30) = 7.91$, $P < 0.01$; for 800–1100 ms, $F(1,30) = 10.42$, $P < 0.005$; for 1100–1400 ms, $F(1,30) = 27.52$, $P < 0.001$]. As is evident from Fig. 3, these interactions

reflect that fact that, in each case, the asymmetry of the old/new effects reversed between frontal and posterior regions of the scalp.

Additional analyses

Two further across-group analyses were conducted on (recollected minus new) difference scores, each motivated by the apparent differences in the onset latencies of the two groups' old/new effects evident in Fig. 2. The first analysis investigated whether these differences in onset were in fact reliable and, if so, whether the differences varied according

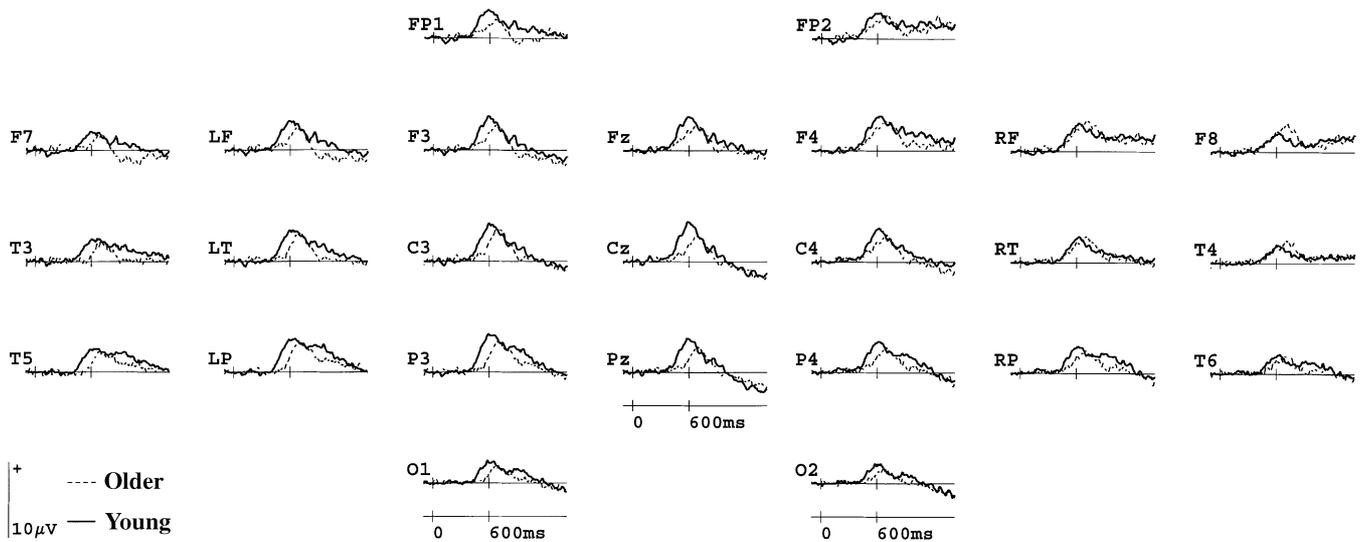


Fig. 2 Grand average subtraction waveforms (recalled minus new) for both the young (unbroken lines) and older groups (broken line). Electrode sites as for Fig. 1.

to electrode site. This analysis was conducted on the mean amplitudes of two consecutive latency regions, 500–600 and 600–700 ms post-stimulus, measured at lateral frontal (LF/RF) and lateral parietal (LP/RP) sites. The first of these regions encompasses the period during which, according to Fig. 2, parietal and left frontal old/new effects are evident only for the young subjects. In the subsequent time window, by contrast, effects are evident at all sites for both subject groups. The data were analysed by ANOVA, employing the factors of group, latency region, location (frontal versus parietal) and hemisphere. Crucially, the ANOVA gave rise to reliable interactions between group and region [$F(1,30) = 4.83$, $P < 0.05$], and between these two factors and hemisphere [$F(1,30) = 6.79$, $P < 0.025$]. These findings indicate that group differences in amplitude are greater for the earlier than for the later region, especially over the left hemisphere. A subsidiary ANOVA confined to the data from the right frontal site revealed no evidence for a group \times latency region interaction [$F < 1$]. By contrast, this interaction was highly reliable in the ANOVA of the data from left parietal electrode [$F(1,30) = 13.08$, $P < 0.005$], reflecting the fact that the differences between the groups in the size of their old/new effects was greater in the earlier than in the later latency region (2.58 μ V versus 0.94 μ V). Together, these results confirm the impression given in Fig. 2 that the onset latencies of the young and older subjects differ by varying amounts at different electrode sites.

In light of these findings, a final analysis was conducted on measures of the old/new effects from each group which took account of the fact that, at many electrode sites, the effects differed in the latency of their onsets and hence their peak magnitudes. To compensate for these differences, the peak amplitudes of the younger subjects' old/new effects were quantified by measuring the mean amplitude of the region between 530 and 630 ms, whereas the effects for the

older subjects were measured as the mean amplitude of the 630–730 ms latency region. ANOVA of these data (factors of group and electrode site) confirmed the findings of the analyses reported in the foregoing section, in that neither the main effect of group, nor the group \times site interaction, approached significance [$F(1,30) = 1.28$ and $F(4.6,138.3) = 1.51$, respectively]. The same finding held when the ANOVA was restricted to data from selected electrodes. For example, analysis of the data from the lateral frontal and lateral parietal electrodes gave rise to no effects involving the factor of group, but did reveal a reliable interaction between location (frontal versus parietal) and hemisphere, reflecting the reversed asymmetries of the old/new effects at the frontal and parietal sites.

Discussion

Behavioural performance

The patterns of performance for the initial recognition decision and the source judgement task were consistent with those found in previous studies (Spencer and Raz, 1995). Older subjects' recognition memory was slightly, but not significantly, lower than that of the young group. By contrast, source memory, measured as the proportion of recognized items that were assigned to the correct encoding context, was markedly lower in the older subjects. Indeed, the scores shown in Table 2 underestimate the magnitude of this difference, as they are uncorrected for the effects of guessing in the absence of knowledge about the source of a recognized item. As estimated by the method employed by Rugg *et al.* (1998), source information was retrieved accurately by the young subjects on ~77% of the trials on which a studied item was correctly endorsed as old, but this figure drops to only 43% in the case of the older subjects. These findings

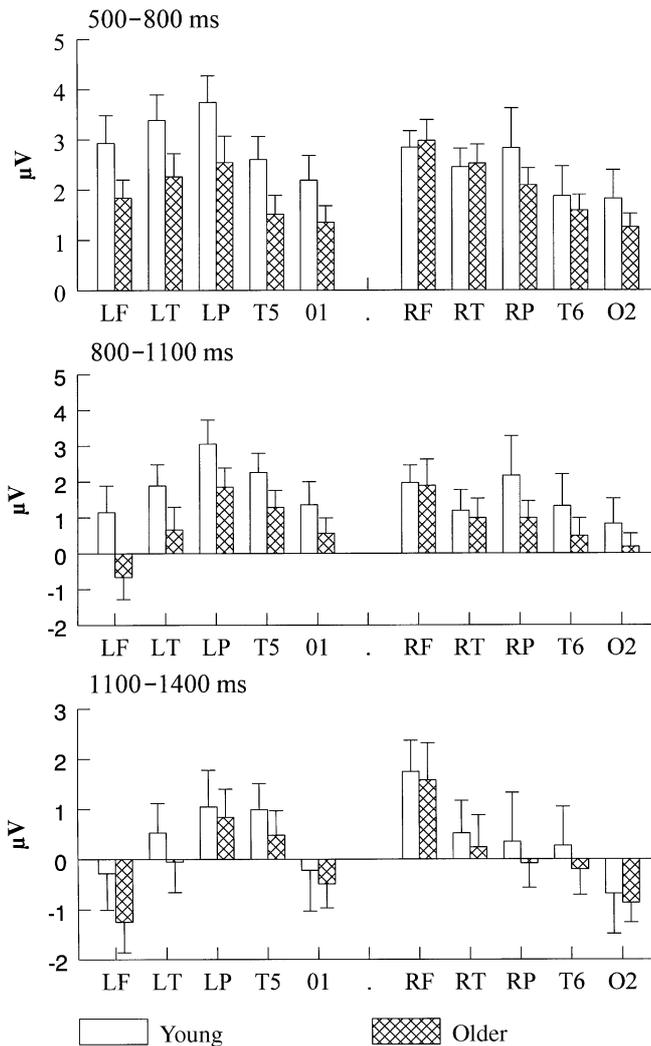


Fig. 3 Mean (and standard error) difference between the amplitudes of the ERPs elicited by recollected and new items in the 500–800, 800–1100 and 1100–1400 ms latency regions, shown separately for each group at selected lateral electrode sites.

are consistent with the proposal that the ability to retrieve contextual information about prior events (recollection) is highly vulnerable to increasing age.

However, the findings from the 'remember/know' task are not consistent with this proposal, in that young and elderly subjects were equally likely to endorse recognized items as having been 'remembered'. The proportion of 'remember' responses made by the young group (77%) was equivalent to the estimated proportion of trials on which the source of the test item was known (see above). By contrast, the proportion of 'remember' responses in the older group (76%) far exceeded the estimated proportion of trials on which source memory was accurate (43%). It follows from these findings that older subjects were willing to endorse items as recollected in the absence of the retrieval of information about the voice or encoding operation associated with the item at study.

The finding of equivalent proportions of 'remember'

responses in young and old groups is not without precedent; of the three experiments reported by Perfect *et al.* (1995), two employed a study task in which subjects were merely instructed to remember words for a subsequent test (similar instructions were employed by Parkin and Walter, 1992), and one required subjects to perform specific encoding tasks at study. An age-related reduction in 'remember' responses was found only in the two experiments in which the study task was unconstrained, a finding consistent with the proposal that elderly subjects are less likely to adopt optimal encoding strategies spontaneously (Craik and Jennings, 1992). In the present experiment, study processing was both highly constrained and elaborative, conditions under which Perfect *et al.* (1995) also failed to find age-related differences in 'remember' responses.

This precedent notwithstanding, the discrepant pattern of findings for the source and 'remember/know' tasks noted above still needs to be explained. One possibility is that relative to the young group, the older subjects adopted a more liberal criterion for categorizing a recognized item as 'remembered'. By this argument, older subjects were more willing to give a remember response on the basis of an impoverished or perhaps even an absent episodic representation of the study event than were the young subjects. An alternative possibility is that the groups of subjects adopted similar criteria in the 'remember/know' task, and responded on the basis of equally strong 'recollective experiences'. The content of these experiences differed between the groups, however, such that they were more likely in the case of the young subjects to include 'differentiated' information (Johnson *et al.*, 1993); that is to say, information about an episode sufficient not only to warrant a 'remember' response, but to support the source discrimination. By this argument, the probability of recollection, in its most general sense, was equivalent for young and elderly subjects; what differed was the specificity of the information that was recollected.

ERPs

The ERPs from both subject groups showed patterns of memory-related effects that were qualitatively similar to those reported in previous studies of source memory (Wilding and Rugg, 1996, 1997a, b). These effects consisted principally of two positive-going shifts. One of these was phasic, left-lateralized and posteriorly distributed (the left parietal old/new effect), while the other was more sustained, right-lateralized, and frontally distributed (the right frontal effect). In accord with the findings of two experiments employing young subjects (Rugg *et al.*, 1998), neither the scalp distributions nor the magnitudes of the memory-related ERP effects in the older subjects differed according to task. The reasons why items defined as recollected in source memory and 'remember/know' tasks should give rise to such similar patterns of brain activity are discussed elsewhere (Rugg *et al.*, 1998). These reasons will not be rehearsed here, other

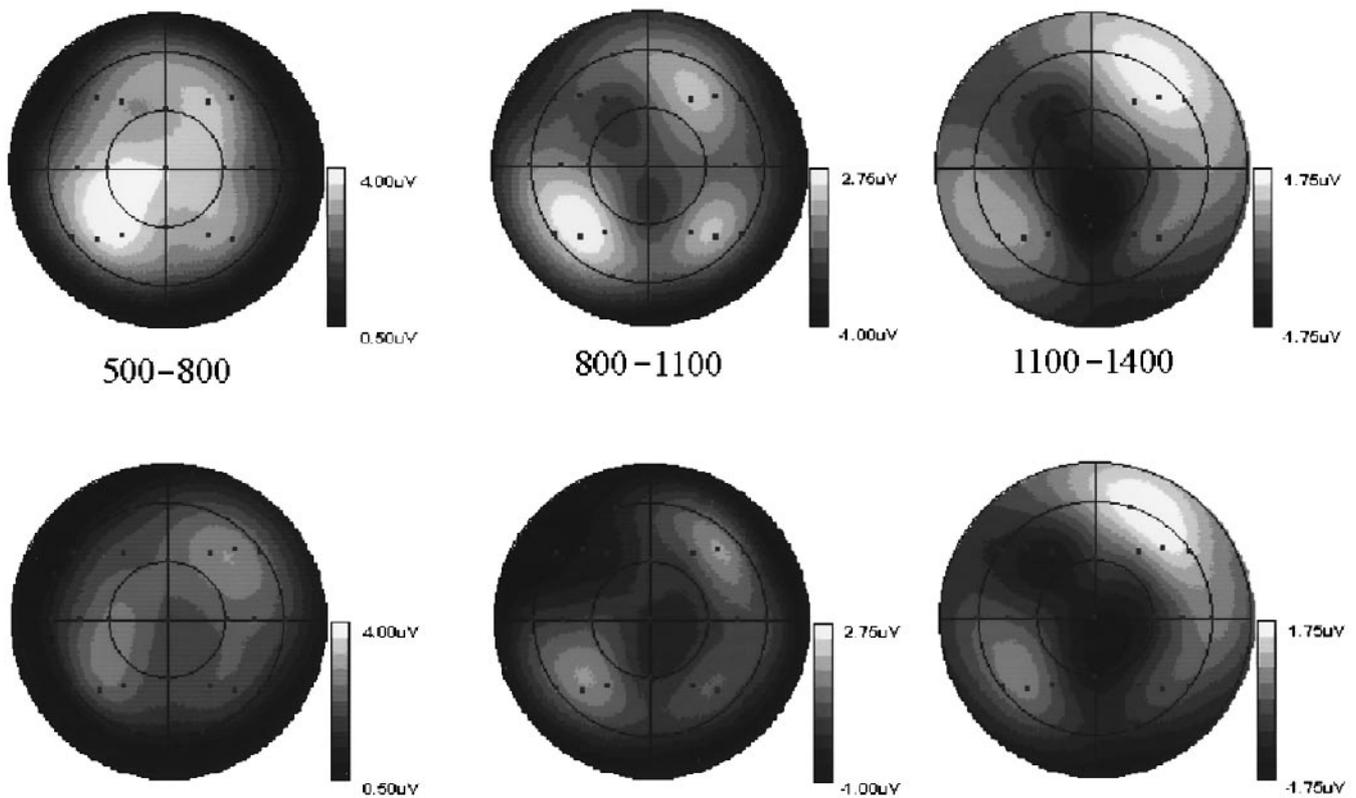


Fig. 4 Spherical spline maps illustrating the scalp topography of the differences between ERPs to recollected and new items in the young group (upper row) and the older group (lower row).

than to say that the findings support previous proposals (Yonelinas and Jacoby, 1995), based on behavioural findings, that 'operational' and 'subjective' methods for identifying trials on which recollection occurred tap functionally equivalent memory processes.

The ERP old/new effects elicited by recollected items in the young and older groups were strikingly similar in respect of their magnitudes and scalp distributions. Thus, when experimental tasks are used that permit the identification of test trials on which recollection is likely to have occurred, and brain activity is sampled from those trials only, there is little evidence to suggest that young and older subjects differ with respect to the identity of the brain regions which are engaged, or the extent to which the regions are activated. These findings stand in contrast to those obtained in two studies (Rugg *et al.*, 1997; Swick and Knight, 1997; but see Friedman *et al.*, 1993) investigating ERP correlates of memory for words repeated over relatively short intervals (in the order of a few seconds to a minute or so) in continuous recognition tasks. In both studies, young subjects' ERPs to correctly classified repeated words ERPs showed a sizeable positive-going shift. In older subjects, by contrast, this effect was greatly attenuated, even when only a very short interval intervened between the first and second presentation of a repeated word. Rugg *et al.* (1997) suggested that the demands of the continuous recognition task, and especially the fact that encoding was unconstrained, led to a failure on the part

of the older subjects to encode words 'deeply', and hence to low levels of episodic retrieval and a near-total dependence on item familiarity to support performance. In the present study, deep encoding was enforced by the nature of the study tasks, and trials were segregated according to whether or not items elicited episodic retrieval.

The present findings are also at odds with a previous ERP study of the effects of age on source memory (Trott *et al.*, 1997), in which it was reported that ERP differences between old and new items showed an age-related reduction at frontal electrode sites. While it is difficult to know which of the many differences between that study and the present one are responsible for the discordant findings, one factor which stands out is the different levels of source memory exhibited by the older subjects. In the study of Trott *et al.* (1977), source accuracy averaged 55%, in contrast to the 71.5% accuracy achieved in the present study. While the difference between these scores may not seem very great, when corrected for guessing (Rugg *et al.*, 1998) they indicate that older subjects in Trott *et al.* (1997) made veridical source judgements on just 10% of trials. By contrast, the subjects in the present study made veridical judgements on ~43% of trials. We suspect, therefore, that the age-related ERP effects reported by Trott *et al.* (1997) may reflect the low proportion of trials on which recollection (as indexed by successful source memory) occurred.

As was mentioned in the Introduction section, it has been

proposed that the left parietal and right frontal old/new effects reflect functionally distinct cognitive operations, with quite different neural bases. The left parietal effect is thought to reflect the outcome of hippocampally mediated episodic retrieval operations, through which information about the encoded event is recovered and made available for further processing. The right frontal effect, by contrast, is thought to reflect the engagement of operations that act on the products of retrieval, integrating these into a representation capable of serving goal-directed behaviour (Moscovitch, 1992). It has further been suggested that the right frontal effect originates in right dorsolateral prefrontal cortex, and that it represents the electrophysiological correlate of the right prefrontal activations reported in numerous functional neuroimaging studies of episodic retrieval (Fletcher *et al.*, 1997).

Interpreted within this framework, the present findings suggest that both hippocampally mediated retrieval operations, and 'post-retrieval' processes supported by the prefrontal cortex, can remain largely unchanged with advancing age. From this perspective, these findings can be seen as lending support to some of the results of three of the four PET studies of age-related effects on memory retrieval cited in the Introduction section. They are in line with the results of Schacter *et al.* (1996) in suggesting that hippocampally mediated retrieval processes are relatively intact in older people, and they also agree with findings (Grady *et al.*, 1995; Backman *et al.*, 1997) that, during retrieval, the right prefrontal cortex is activated equally strongly in young and older subjects. The present results offer no support, however, for the proposal (Cabeza *et al.*, 1997) that the brain activity supporting memory retrieval is, in general, weaker or more diffusely distributed in older people. While this proposal may be true when a retrieval attempt is unsuccessful (not investigated here), our findings suggest that it does not hold when a retrieval cue elicits successful recollection.

It is important not to lose sight of the fact that, despite the similarity of the ERP correlates of successful recollection in older and younger subjects, there were marked differences between the groups in their memory performance. These differences were evident both on standard neuropsychological tests (Table 1) and, more importantly, on the source memory task. In light of the similarity between the two groups in their ERP correlates of successful retrieval, it seems unlikely that this age-related decline in source memory reflects a general degradation of the brain systems supporting this form of memory in the young; were this the case, one might have expected that even when memory was accurate, brain activity would have shown age-related differences. Instead, it appears that the poorer memory of the older subjects reflects a decline in the probability that a test item will elicit successful episodic retrieval. This suggestion is consistent with the idea (Grady *et al.*, 1995; Perfect and Dasgupta, 1997) that the age-related memory decline in episodic memory function is more the

result of changes in the efficiency with which events are encoded than in how they are retrieved.

This conclusion should, however, be regarded as provisional, in that the memory-related ERP effects of the older and young subjects did differ in one potentially important respect. Other than at right frontal electrode sites, the onset latencies of the older subjects' effects were delayed by ~100 ms. An age-related delay in an electrophysiological correlate of a resource-demanding operation such as episodic retrieval is perhaps unsurprising, given the extensive evidence that such operations are, in general, slowed in older subjects (Salthouse, 1996). It is difficult to know what the functional significance of this finding might be in light of the fact that, in all other respects, the memory-related effects of the two groups were very similar. The possibility cannot be ruled out, however, that this delay represents evidence of a functionally significant decline in the efficacy of retrieval operations. It is noteworthy that the one region where the onset of these effects did not differ with age was over the right frontal scalp. On the assumption that these electrodes do indeed detect memory-related activity originating from right prefrontal cortex, this finding underscores the fact that there are at least some circumstances in which the functional integrity of this region appears to be unaffected by advancing age. In addition, the finding adds age to the range of variables that have been found to have dissociative effects on the left parietal and right frontal old/new ERP effects (see also Wilding and Rugg, 1997a; Allan *et al.*, 1998).

There is one other difference between the ERPs of the older and young subjects that should be mentioned. This concerns the differences in the morphology of the waveforms from the two groups. These differences are especially prominent over the anterior scalp, where the older subjects' ERPs are much the more positive-going (cf. Fig. 1A and B). Very similar differences in waveform morphology are evident in the data from previous studies of both direct and indirect memory tests (e.g. Rugg *et al.*, 1994, 1997), indicating that the differences are not peculiar to the experimental tasks employed here. They are in any case difficult to interpret; while they may be functionally significant, they are just as likely to reflect some functionally uninteresting consequence of ageing, such as a change in generator orientation caused by brain atrophy. The key point is that these morphological differences did not interact with the effects of the experimental manipulations; memory-related modulations of the ERP waveforms were remarkably similar in the two groups.

Conclusions

The present findings demonstrate that there at least some circumstances in which brain activity engaged by episodic memory retrieval is relatively impervious to the effects of advancing age. The findings agree with those of Grady *et al.* (1995) and Backman *et al.* (1997) in suggesting that the role played in memory retrieval by the right prefrontal cortex is little affected by age. They therefore challenge accounts of

cognitive ageing (e.g. West, 1996) that posit that any cognitive process supported by the prefrontal cortex will show an age-related decline. Which other prefrontal regions also maintain their functional integrity with advancing age is an important question for future research.

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