Two Hemispheres for Better Memory in Old Age: Role of Executive Functioning

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Abstract

■ This experiment explored the functional significance of age-related hemispheric asymmetry reduction associated with episodic memory and the cognitive mechanisms that mediate this brain pattern. ERPs were recorded while young and older adults performed a word-stem cued-recall task. Results confirmed that the parietal old/new effect was of larger latency and reduced magnitude and less lateralized in the older group than the young group. Correlational and regression analyses indicated that the degree of laterality of brain activity determines the accuracy of memory performance and mediates age-related differences in memory performance among older participants. They also confirmed a cascade model in which the individual level of executive functioning of older adults mediates age-related differences in the degree of lateralization of brain activity, which in turn mediates age-related differences in memory performance. ■

INTRODUCTION

A central challenge facing the cognitive neuroscience of aging is to determine whether age-related changes in brain activity reflect processes that are beneficial, detrimental, or inconsequential to cognitive functions. An intriguing result from brain imaging studies of cognitive aging is evidence of reduced hemispheric asymmetry during aging. The aim of this experiment was to address the controversial issue of the functional significance of this age-related reduction of hemispheric asymmetry phenomenon. By computing an individual index of lateralization of brain activity, correlational and regression approaches were used to investigate directly the relationship between episodic memory performance, executive functioning, and the lateralization of the ERP parietal old/new effect in young and older adults.

Everyday experience converges with experimental observations that advancing age is often associated with a decline in memory abilities (Luo & Craik, 2008; McDaniel, Einstein, & Jacoby, 2008). Previous studies have consistently reported that episodic memory is one of the most affected memory system with increasing age. Neuroimaging studies have often reported an age-related decrease in neural activity during episodic encoding and/or retrieval, which is classically interpreted as a reflection of cognitive impairment (Park & Reuter-Lorenz, 2009; Dennis & Cabeza, 2008; Grady, 2008). In addition to this underactivation, a number of studies have reported unexpected patterns of cerebral reorganization in older adults, such as increased activation in some brain regions or recruitment of additional brain areas, which may reflect either dysfunction or a form of compensation (Park & Reuter-Lorenz, 2009). In particular, one consistent finding of neuroimaging studies on episodic memory is that activations tend to be less lateralized in older than in young adults (Dennis & Cabeza, 2008). This pattern of reduced asymmetry in older adults has been conceptualized in the HAROLD model (hemispheric asymmetry reduction in older adults; Cabeza, 2002). This model has been supported by data from different neuroimaging techniques (TMS, fMRI, and ERP) in several cognitive domains. The HAROLD model was originally used to describe frontal activity, but studies suggest that it may also apply to other brain regions such as parietal or temporal areas (Dennis & Cabeza, 2008). Nevertheless, the functional significance of these changes in laterality remains unclear. According to the compensation hypothesis, contralateral recruitment corresponds to a form of compensatory mechanism to counteract age-related neurocognitive deficits and support task performance. Some studies, in which older adults are divided into groups based on memory performance, have observed strongly lateralized activity in young adults and low-performing older adults, but bilateral activations in high-performing individuals (Daselaar, Veltman, Rombouts, Raaijmakers, & Jonker, 2003; Cabeza, Anderson, Locantore, & McIntosh, 2002; Rosen et al., 2002). However, other studies have found that increased contralateral activation is detrimental to performance (Colcombe, Kramer, Erickson, & Scalf, 2005; Persson et al., 2005). This raises the alternative possibility that the bilateral pattern of activation reflects older adults' difficulty in recruiting specialized neural networks (Buckner & Logan, 2002). The present experiment aimed

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to disentangle these two interpretations of age-related hemispheric asymmetry reduction by directly investigating the correlation between the laterality of neural activity and cognitive performance. Reuter-Lorenz et al. (2000) found a negative correlation between working memory performance and the degree of laterality of pFC activation exclusively in their older group. This finding suggests that a bilateral pattern supports cognitive performance but only in older adults, probably to compensate age-related declines in old age. This kind of study using a correlational approach has never been conducted in the field of episodic memory.

Our experiment also addressed another current issue in the field of neurocognitive aging concerning the cognitive mechanisms that underlie increased neural recruitment in older adults, possibly reflecting compensatory mechanisms. One factor frequently put forward to explain age-related changes, particularly in memory, is executive functioning, referring to high-level cognitive processes that supervise and control other cognitive subprocesses. The executive deficit hypothesis suggests that cognitive impairments during aging result from a specific deterioration of executive functions (Braver & West, 2008; West, 1996). For example, executive abilities have been found to be powerful mediators of age-related differences in episodic memory, particularly in its conscious and strategic aspects (Bugaiska et al., 2007; Taconnat, Clarys, Vanneste, Bouazzaoui, & Isingrini, 2007; Crawford, Bryan, Luszcz, Obonsawin, & Stewart, 2000; Glisky, Polster, & Routhieaux, 1995). We postulate that a high executive level in older adults may result in the implementation of efficient higher-order encoding and retrieval strategies associated with a compensatory brain network such as a more symmetrical pattern of neural activity. Thus, it could be assumed that the supposed compensatory age-related lateralization differences are related to the individual executive functioning level of older adults. We further postulate that executive functioning could mediate age differences in the laterality of neural activity, hence age differences in memory performance among older adults.

This experiment was designed to investigate the nature and strength of the relationship between the degree of lateralization of brain activity associated with episodic memory, executive functions, and episodic memory performance in young and older adults. To this end, ERPs were recorded while young and older participants performed a word-stem cued-recall task. A consistent finding from ERP studies using word-stem cued-recall tasks is that ERPs evoked by correctly completed and recognized stems elicit a positive deflection, in contrast to those evoked by correctly rejected new stems (Wilding & Sharpe, 2003; Friedman & Johnson, 2000; Allan, Wilding, & Rugg, 1998). This difference is called the old/new effect and is assumed to reflect processes that contribute to retrieval success in episodic memory. The parietal old/new effect is the component that has been studied the most. It onsets around 400-msec poststimulus, persists for several hundred milliseconds, is maximal at parietal scalp sites, and is strongly lateralized, classically predominant on the left hemisphere. It is considered as a good index of recollection processes, which correspond to conscious retrieval of contextual details associated with an item. Thus, this ERP effect is well suited to investigate the influence of executive functions, because they are strongly involved in recollection processes (Bugaiska et al., 2007). In addition, this parietal old/new effect has been proved to be age-sensitive because it is often of reduced magnitude and of larger latency in older compared with young adults (Friedman, 2003). This parietal ERP component that appeared classically much more left sided for verbal material in episodic memory (Angel, Fay, & Isingrini, 2010) has been demonstrated to be generated in medial and lateral regions of the parietal lobe so probably reflects brain activity from these brain areas (Rugg & Curran, 2007). Moreover, ERP studies using a recognition task (Duverne, Motamedinia, & Rugg, 2009) and a cued-recall task (Angel, Fay, Granjon, Bouazzaoui, & Isingrini, 2009) have found that the parietal old/new effect is symmetrically distributed over the two hemispheres in older but not in young adults, which is in line with the HAROLD model. Thus, it seems that it could be a good index of the lateralization of parietal brain activity. To investigate the role of executive functioning in the present experiment, participants also performed tests widely used to assess executive abilities.

We used correlation and regression approaches to explore whether the age-related reduction of hemispheric asymmetry was beneficial or detrimental to memory performance. We expected first to confirm age differences in memory abilities, in executive functioning and in the old/new effect (latency, magnitude and lateralization), by comparing young and older adults. We assumed to observe poorer performance in the memory task and in executive tests for older than young adults. On the basis of previous works, we also hypothesized that the parietal old/new effect should be delayed and of reduced magnitude in the older compared with the young group. We aimed to test whether the age-related reduction of hemispheric asymmetry of the parietal old/new effect could be observed with our specific word-stem cued recall task. Consistently with the HAROLD model and with previous studies, we expected to observe a more symmetrically distributed parietal old/new effect in the older group than in the young group. In addition, we also investigated age differences in lateralization by computing a lateralization index of the parietal old/new effect for each individual based on left and right hemisphere activation differences. We postulated that, if this ERP index is indeed a good lateralization index of brain functioning, it should be smaller in older adults compared with young adults, reflecting the age-related reduction of hemispheric asymmetry. On the basis of the work by Reuter-Lorenz et al. (2000) and on the HAROLD model, we hypothesized that in the older group, the degree of lateralization of the parietal old/new effect should decrease with increasing age and that greater symmetry should be associated to better memory abilities. We did not expect to observe correlations of the lateralization index with age or memory performance in the young group because the beneficial effect of the reduction of hemispheric asymmetry is supposed to occur over an advanced age. On the basis of the results from correlation analyses, regression analyses were then conducted. Consistent with the compensation hypothesis, we assumed that the degree of lateralization of the parietal old/new effect would mediate age-related differences in memory performance among older adults. Correlation and regression analyses also enabled us to examine the role of executive functioning in the relationship between age, memory, and the ERP lateralization index. We assumed to confirm that, in older adults, executive functioning should be related to age and memory but also to the degree of lateralization of the ERP old/new effect. More precisely, executive functioning was expected to be a powerful mediator of age differences in memory among older adults, consistently with previous studies. We also aimed to test the executive hypothesis of brain reorganization, which proposes that the executive functioning of older adults would account for the age-related variance in the degree of lateralization of brain activity, which then would mediate age differences in memory performance.

METHODS

Participants

Participants were 25 young adults (11 men, 14 women) aged between 22 and 26 years and 28 older adults (10 men, 18 women) aged between 60 and 80 years. Participants' characteristics in each age group are summarized in Table 1. The two groups had an equivalent level of education ($t(51) = 1.25$), but older adults obtained higher scores than young adults to the Mill Hill vocabulary test (Deltour, 1993) ($t(51) = -4.66$, $p < .001$), as it is classically observed in the cognitive aging literature. All subjects were right-handed (Edinburgh Inventory; Oldfield, 1971) native French speakers with normal or corrected-to-normal vision. They reported themselves to be in good physical and mental health and not taking medication known to affect the CNS. All older adults obtained a score above 27 on the Mini-Mental State Examination (Folstein, Folstein, & McHugh, 1975). All participants signed an informed consent form before the beginning of the experiment.

Table 1. Characterictics of the Young and Older Groups

	Young, n = 25	*Older, n = 28*	*t(51)*
Age	24.44 (1.12)	67.1 (5.64)	−37.32*
Education	13.04 (3.71)	11.83 (3.39)	1.25
Mill Hill test	23.6 (5.37)	29.07 (3.10)	−4.66*

*$p < .001$.

Material and Procedure

In the first session, participants were administered neuropsychological tests. The WCST, the Stroop test, and the excluded letter fluency test (ELFT) were chosen to assess multidimensional executive functional abilities such as inhibition or switching functions. In the second session, ERPs were recorded while participants completed a cued-recall task.

Executive Tests

WCST (Heaton, Chelune, Talley, Kay, & Curtiss, 1993). In this test, participants had to sort cards differing in color, number, and/or shape by deducing the sorting criterion from feedback given by the experimenter. The score was the widely employed number of perseverative errors, which is the most age-sensitive measure. Perseverative errors on the WCST constitute a good indicator of a deficit of switching abilities related to this task.

The Stroop color–word test (SCWT; Stroop, 1935). This test is commonly used to assess inhibition abilities. Two subtests of the standard SCWT were used in the present experiment: the color subtest (C), in which participants had to name the color of crosses (XXX), and the color–word interference (CW) subtest in which they had to name the color of color–words while ignoring the printed word. The number of correct responses in 45 sec was recorded for each condition. The score was the measure of interference, computed as follows: [(Score C − Score CW) / Score C] (Li & Bosman, 1996). Higher scores indicate lower inhibition abilities.

ELFT (Bryan, Luszcz, & Crawford, 1997). This test is commonly used to assess particularly inhibition and switching abilities. In this test, participants were asked to say aloud in 1 min as many words as possible not containing the letter A in the first trial and not the letter E in the second. The score was the total number of correctly produced words under the two conditions.

Experimental Task

Stimuli in the ERP task were 180 six- to ten-letter words. The stem (first three letters) was different for each word. Each stem could be completed by at least five different words, and the target word was never the most frequent. Participants performed a word-stem cued-recall task consisting of three study test blocks. The pool of words was divided into three lists of 60 words, one for each block. Each list was further divided into three sublists. The mean number of letters, the mean number of possible candidates, and the mean frequency of occurrence (Brulex database; Content, Mousty, & Radeau, 1990) were equivalent in each list and in the three sublists. During each study phase, 44 items were presented, 40 extracted from two sublists, with two additional items at the beginning and two at the end of each study list to reduce the risk of primacy and recency effects. The study task was to learn each target item and to judge whether the word was concrete or abstract. In each trial, a fixation cross was presented for 1 sec, after which the target word appeared for 500 msec. The screen was then blanked for 1 sec, followed by a question mark displayed for 2 sec, during which time participants gave their answer orally. The screen was blanked again for 1 sec, and then the next trial began. Each test phase comprised 60 word-stems, 20 from the nonstudied sublist and the remaining 40 from the study list. The sublist used for "new" items was counterbalanced across subjects. The memory test consisted in completing each stem with a studied word, or failing that, with another suitable word, and then indicating whether the completion corresponded to a studied (old) or an unstudied (new) word. Each test trial began with a fixation cross displayed for 1 sec and then removed 120 msec before the test item was shown for 500 msec. The screen was blanked for 1.5 sec, then the question mark appeared for 3 sec. Participants had to answer aloud as quickly and accurately as possible during that time. The next trial began 2 sec later.

EEG Recording and Analysis

Continuous EEG was recorded during the test phases of the cued-recall task, using 62 electrodes placed on the scalp in accordance with the international 10–20 system (Jasper, 1958). All recordings were referred to linked mastoids, and a ground electrode was placed on an anterior site (AFz). A vertical electrooculogram was obtained from an electrode below the right eye, and a horizontal electrooculogram from an electrode placed at the outer canthus of the left eye. EEG and EOG were digitized at a sampling rate of 512 Hz.

Continuous EEG was epoched off-line with a 200-msec prestimulus baseline and a 1500-msec poststimulus period. Blink artifacts were corrected with Gratton and Coles' algorithm (Gratton, Coles, & Donchin, 1983). Single trials were inspected and excluded from averaging if they contained muscular or other recording artifacts. ERPs were computed for each age group separately for two conditions: correctly completed and recognized stems (old items) and stems (from unstudied items) completed with unstudied words and correctly rejected (new items). The mean number of artifact-free epochs in each experimental condition was respectively for the young group (old [24.4; range = 16–39], new [32.5; range = 16–56]) and for the older group (old [21.86; range = 16–42], new [28.62; range = 17–46]). The number of epochs was significantly higher for the new than the old condition ($F(1, 51) = 31.22$, $p < .001$) but the effect of age ($F(1, 51) = 2.4$) and the age by condition interaction were not significant ($F(1, 51) = 0.25$).

RESULTS

Behavioral Analyses

Age-related differences in memory performance were analyzed through *t* tests computed on different behavioral indexes summarized in Table 2. Analyses revealed that the hit rate (proportion of stems completed by a studied item and correctly judged as old) was significantly higher in the young group than the older group. For the correct rejection rate (proportion of new stems completed by an unstudied word and correctly judged as new), there was only a marginally significant difference in favor to the young group. The false alarm rate (proportion of stems completed by an unstudied word and falsely judged as old) and the baseline rate (proportion of unstudied stems completed by chance with words belonging to the experimental pool) did not significantly differ between the two age groups.[1]

t tests were also performed to compare young and older adults' performance to executive tests (Table 2). To reduce the executive functioning data for subsequent analyses, we conducted a PCA on the three executive tests scores, which showed that the three measures loaded on a same factor. The factor loadings were −.79, −.82, and .75 for the WCST, the Stroop test, and the ELFT, respectively. Then, by computing the average of the standardized *z* scores from the three executive tests, a composite executive functioning index (EFI) was produced, giving

Table 2. Memory Performance in the Cued-Recall Task and Scores to Executive Tests

	Young	*Older*	*t(51)*
Hit rate	0.37 (0.07)	0.28 (0.09)	4.19**
Correct rejection rate	0.83 (0.09)	0.76 (0.16)	1.76 (0.08)
False alarm rate	0.06 (0.05)	0.09 (0.08)	−1.46
Baseline rate	0.06 (0.03)	0.07 (0.05)	−1.44
WCST	7.48 (3.57)	17.21 (8.98)	−5.07**
Stroop	0.34 (0.07)	0.47 (0.11)	−4.78**
ELFT	26.28 (7.74)	22.03 (6.53)	2.18*
EFI	0.52 (0.58)	−0.56 (0.64)	6.47**

Hit rate = proportion of stems completed by a studied item and correctly judged as old, Correct rejection rate = proportion of new stems completed by an unstudied word and correctly judged as new, False alarm rate = proportion of stems completed by an unstudied word and falsely judged as old, Baseline rate = proportion of unstudied word-stems that were completed by chance with words belonging to the experimental pool.

*$p < .05$.

**$p < .001$.

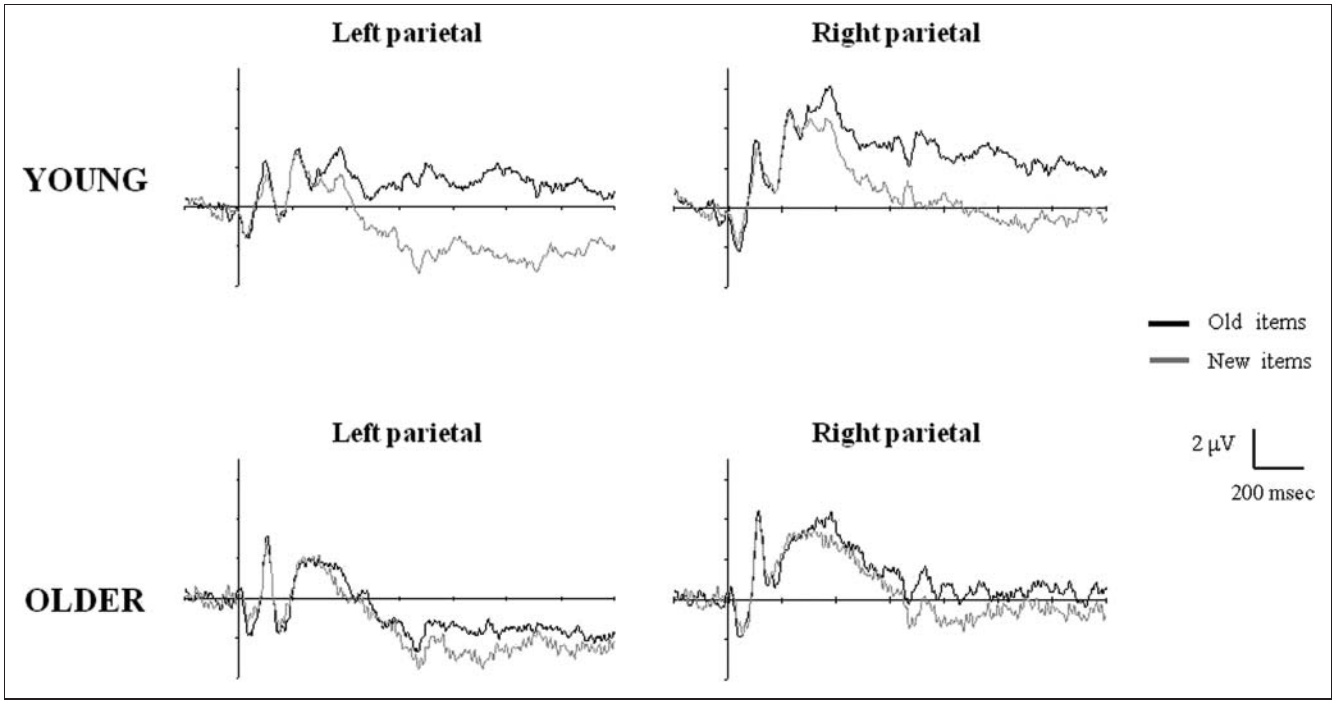

Figure 1. Grand average ERPs associated with old and new items at left parietal and right parietal electrode sites in each age group.

an estimation of each participant's executive functioning level (Glisky et al., 1995). A high score on the EFI indicates good level of executive functioning. Younger obtained better scores than older adults on each of the three individual executive tests and also on the EFI.

ERP Analyses

Figure 1 shows grand average ERP waveforms for old and new conditions in each age group at left and right parietal electrode sites.

First, to investigate the reliability of the old/new effect in our sample, we performed ANOVAs on ERP data from the 22 parietal electrode sites, with factors of Item Type (old vs. new), Hemisphere (left vs. right), and Age (young vs. older) on the mean amplitude of five time windows (400–600 msec, 600–800 msec, 800–1000 msec, 1000–1200 msec, and 1200–1400 msec), broadly consistent with those used in previous studies (Table 3). Post hoc Bonferroni tests were used when necessary. A main effect of Item Type was significant on all time windows. Analyses also revealed a significant Item Type × Age interaction for the 400–600 msec, 800–1000 msec, and 1200–1400 msec epochs. Subsequent analyses in the earliest and the latest periods showed that the effect of Item Type was significant only in the young group. In addition, in the 800–1000 msec epoch, the Item Type effect was of greater magnitude for young adults compared with older adults. An interaction between factors of Item Type, Age, and Hemisphere was significant between 600–1400 msec (Figure 2). This interaction reflected lateralization differences in the parietal old/new effect between the two age groups: The old/new effect was larger at left than right hemisphere sites in the young group whereas it was symmetrically distributed over the two hemispheres in the older group. To investigate whether these lateralization differences significantly differed throughout the recording epoch, we introduced the Time Window factor (400–600 msec,

Table 3. Results of ANOVAs Comparing the Parietal Old/New Effect (from All 22 Parietal Electrode Sites) between the Young and the Old Groups

	Item Type	*Item Type × Age*	*Item Type × Age × Hemisphere*
400–600 msec	$F(1, 51) = 10.94$; $p < .01$	$F(1, 51) = 11.24$; $p < .01$	$F(1, 51) = 1.89$
600–800 msec	$F(1, 51) = 22.84$; $p < .001$	$F(1, 51) = 2.49$	$F(1, 51) = 5.67$; $p < .05$
800–1000 msec	$F(1, 51) = 28.41$; $p < .001$	$F(1, 51) = 6.58$; $p < .05$	$F(1, 51) = 5.36$; $p < .05$
1000–1200 msec	$F(1, 51) = 24.36$; $p < .001$	$F(1, 51) = 0.53$	$F(1, 51) = 5.16$; $p < .05$
1200–1400 msec	$F(1, 51) = 10.78$; $p < .01$	$F(1, 51) = 5.11$; $p < .05$	$F(1, 51) = 4.35$; $p < .05$

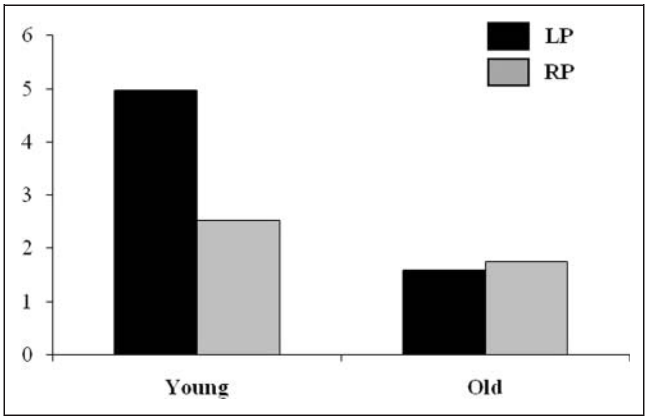

Figure 2. Mean amplitude of ERP old/new effects at right and left parietal scalp sites for the 600–800 msec time window according to age group. RP = right parietal, LP = left parietal.

600–800 msec, 800–1000 msec, 1000–1200 msec, and 1200–1400 msec). This factor did not interact with Item Type, Age, and Hemisphere ($F(4, 204) = 0.59$).

Subsequent analyses were performed on the difference scores (old minus new). Second, to investigate the relationship between the degree of lateralization of the parietal old/new effect and other target variables (age, EFI, memory performance), we computed a parietal lateralization index (PLI) using the formula (Wilke & Lidzba, 2007; Binder et al., 1995):

$$\mathrm{PLI} = |(\sum \text{Left old/new effect} - \sum \text{Right old/new effect})/(\sum \text{Left old/new effect} + \sum \text{Right old/new effect})|.$$

A high PLI value represents a strong lateralization of the old/new effect, whereas a low value corresponds to a more symmetrical distribution. Given that age-related lateralization differences did not differ according to time window, a PLI of the parietal old/new effect was calculated for each individual, for the time window on which the old/new effect was significant for both the young group and the older group (600–1200 msec).

The result of the t test on the PLI confirmed that the parietal old/new effect was less lateralized in the older group than in the young group (young: PLI = 0.66 (0.22), older: PLI = 0.43 (0.24); $t(51) = 3.63$, $p < .001$).

Relationships between the PLI and age, memory performance (as indexed by the Hit rate), and the EFI for each age group are presented in Figure 3. Analyses on data from the young group did not reveal any significant correlations between age, memory performance, EFI, and PLI (see Table 4). In the older group, correlational analyses showed that age was negatively correlated with memory performance and with the EFI (see Table 5). Increasing age was associated with a decrease in memory and executive abilities. Memory performance and EFI were correlated with the PLI. These correlations show that a more symmetrical distribution of the old/new effect was related to a higher level of memory performance and of executive abilities in older adults. Finally, the EFI and memory performance were highly correlated, indicating that older participants with a high level of executive functioning also exhibited good memory performance.

Correlational analyses in our sample of older adults revealed strong relationships between memory performance, age, EFI, and PLI. To identify the best cognitive model accounting for episodic memory performance in old age, we conducted a series of stepwise ascendant regression analyses on data of the older group (see Table 6). Regression analyses were computed first to examine the respective mediating effects of the degree of lateralization (PLI) and executive functioning (EFI) on the relationship between age and memory performance (Models 1–4). Another series of regression analyses were computed to examine whether executive functioning (EFI) could also mediate age-related variance in the degree of lateralization (PLI) (Models 5 and 6).

Age predicted 28% of the variance in memory performance of older adults when entered alone (Model 1). Model 2 showed that when age and PLI were entered in the equation, only PLI proved to be a reliable predictor, accounting for 34% of the variance related to memory performance and that age did not continue to account significantly for this variance. Model 3 showed that when age and EFI were entered in the equation, only EFI proved to be a reliable predictor, accounting for 51% of the variance related to memory performance and that age did not continue to account reliably for this variance. When age, PLI, and EFI were entered in the equation in Model 4, only EFI proved to be a reliable predictor, accounting for 51% of the variance related to memory performance, and age and PLI did not continue to account reliably for this variance. These results suggest that age-related variance in memory performance is mediated by the PLI and executive functions, but this later factor seems to be the best predictor.

The second series of analyses examined age and EFI as predictors of the PLI variance (Models 5 and 6). In Model 5, age accounted for 24% of the PLI variance when entered as sole predictor. Model 6 showed that when age and EFI were entered in the equation, only EFI proved to be a reliable predictor, accounting for 32% of the PLI-related variance and that age did not continue to account significantly for this variance.

DISCUSSION

First, we confirmed age differences in cognitive performance (memory and executive functioning) and in the parietal old/new effect. Behavioral data showed that older adults performed less well than younger subjects on our word-stem cued-recall task, which is consistent with the well-known decline of episodic memory abilities with increasing age (McDaniel et al., 2008). We also found

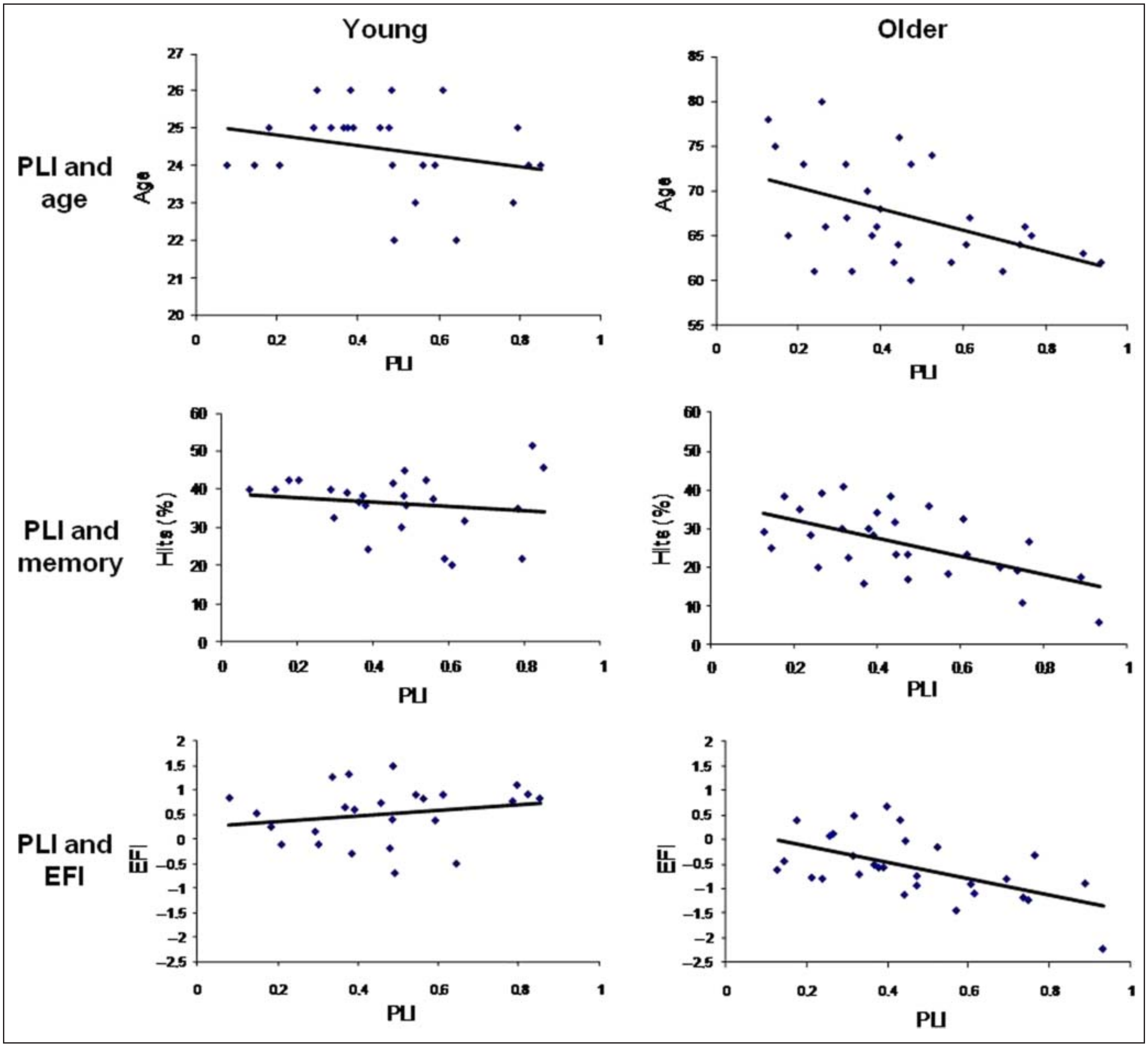

Figure 3. Scatter plots showing relationships between the PLI (600–1200 msec) and age, memory performance, and the EFI for each age group.

the classical executive function deficit associated with age (Braver & West, 2008). At an electrophysiological level, we demonstrated that the parietal old/new effect appeared later and was smaller and less lateralized in the older group than in the young group. The differences in the parietal old/new effect according to age are in agreement with previous findings (see Friedman, 2003, for a review).

Table 4. Bravais–Pearson Correlation Coefficients between the PLI, Age, Memory Performance, and EFI for the Young Group

Variables	*Age*	*Memory Performance*	*EFI*
Age	–	−0.05	0.17
EFI	0.17	0.22	–
PLI 600–1200 msec	−0.001	0.14	0.16

Moreover, the age-related lateralization difference was confirmed by correlational analyses showing that the degree of lateralization of brain activity decreases with increasing age in our sample of older adults. It is the first study to show a linear relationship between age and the

Table 5. Bravais–Pearson Correlation Coefficients between the PLI, Age, Memory Performance, and EFI for the Older Group

Variables	*Age*	*Memory Performance*	*EFI*
Age	–	−0.53**	−0.64**
EFI	−0.64**	0.71***	–
PLI 600–1200 msec	−0.49**	−0.58**	−0.56**

**$p < .01$.

***$p < .001$.

Table 6. Regression Analyses in the Older Group Predicting (1) Memory Performance by Age, EFI, and PLI and (2) PLI by EFI and Age

Dependent Variable	*Regression Model*	*Variables*	R^2	R^2 *Change*	*p*
Memory performance	1	Age alone	.28	.28	<.01
	2	PLI	.34	.34	<.001
		Age	.41	.07	.08
	3	EFI	.51	.51	<.001
		Age	.55	.04	*ns*
	4	EFI	.51	.51	<.001
		PLI	.56	.05	*ns*
		Age	.58	.02	*ns*
PLI	5	Age alone	.24	.24	<.01
	6	EFI	.32	.32	<.01
		Age	.38	.06	*ns*

ns = not significant.

degree of lateralization. Because, neuroimaging studies suggest that the parietal ERP old/new effect reflects activity from parietal areas, our findings confirm that hemispheric asymmetry reduction may be observed in parietal areas (Angel et al., 2009; Duverne et al., 2009; Cabeza, 2002). They support the HAROLD model (Cabeza, 2002) and replicate numerous findings of reduced asymmetry with increasing age (Dennis & Cabeza, 2008). In the young group, the degree of lateralization was not correlated to age. However, the age range was smaller in the young group (20–26 years) than in the older group (60–80 years); thus, the lack of correlation between age and the lateralization index may result from a low level of age variability in this group. Thus, it would be of interest to examine the evolution of the degree of lateralization of brain activity in a long lifespan perspective, especially from 20 to 60 years old to determine when the process of reduction of hemispheric asymmetry with age begins.

The main objective of this experiment was to shed light on the functional significance of reduced asymmetry in old age. We observed that memory performance in the older group was strongly correlated with the degree of lateralization of the parietal old/new effect, indicating that more symmetrical patterns of brain activity during aging are associated with higher levels of memory performance. The finding of a relationship between lateralization and verbal episodic memory appears consistent with the hypothesis of a material-specific lateralization of brain systems for memory that postulates a hemispheric dominance for memory that depends on the kind of material (verbal vs. nonverbal; Opitz, Mecklinger, & Friederici, 2000). Overall, this observation is consistent with the idea that old/new effect cans be used as a relevant index of brain activity lateralization. Interestingly, Elward and Wilding (2010) have demonstrated a relationship between the parietal ERP old/new effect and memory performance founding a correlation between the magnitude of the parietal effect and working memory performance. Nevertheless, this is the first time that the degree of lateralization of the parietal old/new effect has been directly related to performance levels in the field of episodic memory using a correlational approach. Regression analyses further showed that the contribution of age to memory variance among old adults no longer reached significance after statistical control of the lateralization index, in line with the compensatory view (Table 6, Model 2). Thus, the degree of laterality of brain activity is associated to the accuracy of memory performance and mediates age-related differences in memory performance among older adults. Increased symmetrical distribution of brain activity may reflect a response to detrimental changes in aging, serving to mitigate cognitive decline. It is possible that older adults compensate for their difficulties by using alternative cognitive strategies, leading to a hemispheric reorganization. For instance, recent studies suggest that the right hemisphere may be biased to focus on the physical form, in other words on perceptual features of items, whereas the left hemisphere may process information at a more conceptual level (Angel, Isingrini, et al., 2010; Evans & Federmeier, 2007; Marsolek, Nicholas, & Andresen, 2002; Marsolek, 1999). One can speculate that older adults would have difficulties to implement conceptual processes so would rely more strongly on perceptual processes, leading to a less left lateralized pattern of the parietal old/new effect. An alternative explanation is to suggest that older adults need to use both hemispheres more symmetrically to implement the same cognitive operations as young adults.

On the other hand, it is worth noting that in young adults, memory performance was not related to the degree of lateralization of the parietal old/new effect. This finding suggests that the pattern of a symmetrical parietal old/new effect becomes only beneficial to memory performance in old age. An alternative possibility is that young adults could also benefit from symmetrical patterns of brain activity but only at higher levels of task difficulty, when the need for resource-dependent processes becomes higher (for instance by increasing memory load), as suggested by the CRUNCH model (compensation-related utilization of neural circuits hypothesis; Reuter-Lorenz & Lustig, 2005). This idea is supported by findings showing that young adults use both hemispheres only for the most complex conditions (e.g., Cappell, Gmeindl, & Reuter-Lorenz, 2010; Schneider-Garces et al., 2009; Reuter-Lorenz, Stanczak, & Miller, 1999). Thus, additional recruitment would be a normal response to increased task demands. If this hypothesis is true, correlation between memory performance and the degree of lateralization should appear in young adults when task difficulty increases.

Another aim was to investigate the cognitive operations associated with reduced asymmetry during aging. Our results emphasize the role of executive functioning. First, as predicted by the executive deficit hypothesis (Braver & West, 2008; West, 1996), executive functions strongly mediated age-related differences in episodic memory abilities in the older group (Table 6, Model 3). This confirms that executive functions are a powerful predictor of cognitive aging, especially in memory (Bugaiska et al., 2007; Taconnat et al., 2007; Crawford et al., 2000; Glisky et al., 1995). Conversely, in the young group, executive functions were not related to episodic memory performance, suggesting that young adults rely less than older ones on executive functions to perform the task. It must be noticed that the variance of the Hit rate and the EFI did not significantly differ between young and older adults so the lack of correlation involving memory performance or executive functioning in the young group is unlikely to be because of the a lack of variance in memory or executive abilities. However, based on the CRUNCH model, this correlation could appear at higher levels of task demands. This hypothesis would be consistent with the study by Elward and Wilding (2010), who found in young adults a correlation between memory scores and working memory performance, classically viewed as closely related to executive functions (McCabe, Roediger, McDaniel, Balota, & Hambrick, 2010), in an exclusion memory task, which is more effortful than our word-stem cued recall task. Second, in the group of older adults, executive functions were related to the PLI. Older individuals with the highest executive level exhibited the most symmetrical distribution of the parietal old/new effect. This results confirmed the idea that greater symmetrical pattern is associated to better cognitive abilities in older adults but not in younger adults. Third, regression analyses in the older group revealed that the PLI did not add significant contribution to age-related variance in memory performance after executive functioning had been taken into account (Table 6, Model 4). Moreover, the executive functioning level of older adults mediated age-related variance in the degree of lateralization of the parietal old/new effect (Table 6, Model 6). These results are consistent with a neurocognitive cascade view that individual executive functioning capacity of older adults is responsible for the brain reorganization process occurring during aging, which in turn mediates age-related differences in memory performance. A possible explanation is that age-related neurobiological damage induces changes in processing strategy. Older adults with a high executive functioning level may be able to rely on these abilities to successfully implement alternative strategies, leading to functional reorganization through plasticity mechanisms (Greenwood, 2007) such as symmetrical hemispheric recruitment. This "cascade" model is consistent with Reuter-Lorenz and Cappell's (2008) proposal that executive functions are the primary means by which brain functioning is reorganized to compensate for age-related deficits. These findings provide some insights for the question of whether hemispheric asymmetry reductions during aging have a neuronal or a psychological origin (Cabeza, 2002). According to a neurogenic view, age-related lateralization differences would result from changes in neural architecture whereas the psychogenic view postulates that these age-related brain modifications reflect the use of different cognitive strategies. Our results tend to favor the psychogenic interpretation, because older adults' executive functioning level would induce differences in cognitive strategies, reflected in lateralization differences.

It must be noticed that although we used in this experiment an ERP index of parietal activity, the age-related reduction of hemispheric asymmetry has also been demonstrated on frontal areas in numerous studies (Dennis & Cabeza, 2008; Cabeza, 2002) so one can wonder whether a similar pattern of results would be found with an index of frontal activity. As executive functions are also strongly related to frontal functioning, it seems very likely that the level of executive functioning would also determine the degree of lateralization of frontal activity and that greater frontal bilateralization would be associated to better memory performance, consistently with the cascade model we have proposed. Moreover, according to the PASA model (posterior anterior shift in aging; Dennis & Cabeza, 2008), one can expect that the relationships between frontal and parietal activation in aging could differ according to the level of task demands. At low levels of task demands, increased symmetrical distribution in older adults may be observed on both frontal and parietal areas but as task demands reach resource limitations, parietal activations would be reduced in older adults and the symmetrical distribution would be observed only on frontal areas, helping to compensate for parietal deficits, as predicted by the PASA model (Dennis & Cabeza, 2008). It would be interesting to directly investigate these hypotheses by examining simultaneously ERP lateralization indexes of both frontal and parietal areas. Three important conclusions emerge from the present study. First, we have shown that a symmetrical pattern of brain activity contributes to successful episodic memory performance, specifically in old age. Secondly, this pattern mediates age-related differences in memory performance among older adults, adding weight to the compensation hypothesis. Thirdly, executive functioning level of older adults emerged as a powerful mediator of age-related differences in both episodic memory performance and the degree of lateralization. Thus, increased brain recruitment may reflect efficient memory strategies based on good executive functioning, leading to better memory performance. This strongly suggests that cognitive abilities may determine brain reorganization during aging, in line with the psychogenic view. Interestingly, recent studies have demonstrated the possibility to improve older adults' executive functions thanks to training programs (Dahlin, Nyberg, Bäckman, & Neely, 2008). These findings provide an optimistic view of cognitive aging, supporting the idea that improving individual executive abilities could lead to a better use of brain compensatory mechanisms allowing older individuals to show only modest losses or even maintain functioning with age.

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Note

1. An additional analysis showed that the conditional rate of recognition (mean probability of correctly recognizing a correct completion) was statistically greater than a rate of 0.50 in each age group. This result indicates that performance in the memory task was statistical greater than chance.

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