Differences in EEG power in young and mature healthy adults during an incidental/spatial learning task are related to age and execution efficiency

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Abstract The differential characteristics of absolute power in the EEG theta (4–8 Hz) and gamma (30–45 Hz) frequency bands have been analysed in young (18–25 years old, $n=14$) and mature adults (45–65 years old, $n=12$) during the incidental or intentional behavioural conditions of learning and recalling in a visuospatial task. A printed drawing of a maze including eight figures of common objects in specific placements, solved by connecting its entrance and exit points, allowed the subject's performance efficiency to be measured based on the number, position accuracy and/or identity of incidentally or intentionally learned and remembered objects. Meanwhile, EEG recordings from frontal, parietal and temporal derivations were obtained to determine the power values of the theta (4–8 Hz) and gamma (30–45 Hz) bands for each behavioural condition and derivation. Relative to the young adults, the mature adults generally showed lower absolute theta power values,

mainly due to their low theta powers under the basal and incidental learning conditions, and higher absolute gamma power values in the frontal and temporal regions. Furthermore, higher theta band power in the frontal regions was related to higher performance efficiency in both incidental and intentional learning, regardless of the subjects' age. A significant negative correlation between the parameters of individual incidental or intentional learning performance and age was also found. Indeed, a differential accuracy of remembered information seems to be associated with age and incidental or intentional learning/memory testing conditions. These data support an increasing vulnerability of visuospatial learning abilities at mature ages and as ageing progresses.

Keywords Incidental learning · Intentional learning · Spatial learning · Age · Theta activity

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Introduction

Information concerning daily events may be acquired in the absence of an intentional, conscious purpose, thereby allowing learning and, eventually, remembering. However, conscious processes are required for the retrieval of information, which is acquired through this incidental learning, from episodic memory (Rugg et al. 1997).

It is well established that the participation of the temporal and frontal lobes in information encoding and retrieval processes account for episodic memory (Gabrieli et al. 1997; Rombouts et al. 1997; Stern et al. 1996), although the left prefrontal cortex appears to be mainly involved in episodic information encoding processes, while the right prefrontal cortex is mainly involved in its retrieval (Tulving et al. 1994). Because some episodic information is incidentally acquired, some researchers have questioned the participation of the same cerebral structures and similar neural processes in encoding both episodic and incidental information.

Neuro-imaging studies (fMRI) have demonstrated the participation of the temporal medial lobe structures in the encoding of memory. This has been shown by the greater activation of these brain structures during the acquisition of either intentional or incidental information from novel items and during its retrieval than during the same processes when familiar items are used. In addition, activation of the temporal medial lobe structures appears to be differentially lateralized according to the type of acquired or retrieved information (Brewer et al. 1998; Martin 1999; Stern et al. 1996; Strange et al. 2002; Wagner et al. 1998).

The activation of different cerebral regions has been compared by observing changes in the regional cerebral blood flow in subjects during the recall of words that have been either intentionally or incidentally learned. In this way, hippocampal activation was related to the successful remembering of an item independent of learning intentionality. Meanwhile, remembering incidentally learned words was related to the activation of the left/right lateral parietal cortex and right frontopolar cortex (Rugg et al. 1997). However, it has also been observed that the encoding of incidentally learned information takes place within the same cerebral structures, that is, the hippocampal region and perirhinal and parahippocampal cortices of the temporal medial

lobe, found to be involved in the encoding of intentional learning (Stark and Okado 2003). BOLD fMRI has shown a differential activation of several brain structures between young and old people during the encoding of information of scenes in a task involving incidental learning. In this task, subjects were instructed to categorize scenes (indoor or outdoor). Relative to young subjects, old subjects demonstrated lower activation in the left hippocampus but higher activation in the prefrontal cortical regions. However, this was observed after matching the subjects by performance; both old and young subjects attained a similar efficiency in solving the task (Sambataro et al. 2012).

These findings identify differences in regional brain activation that appear to be age-related, but their association with the performance efficiency in the incidental learning task is unknown.

EEG studies have shown that electrical activity is correlated with intentional learning during both the encoding and the retrieval of learned words lists as well as those of semantic or visuospatial information. Thus, correlations between EEG theta and gamma power and memory performance have been consistently reported (Klimesch 1999; Klimesch et al. 1996). It has been proposed that several aspects of theta activity are involved in the sustained attention to and maintenance of information in working memory (increasing power with increasing memory load) as well as in episodic encoding and retrieval (transient increase of theta power as a consequence of event-related synchronization, mainly in parietal sites) (Klimesch 1999; Klimesch et al. 2010). Additionally, an increase in the theta oscillations in temporal regions preceding the presentation of a stimulus predicts its successful encoding (Guderian et al. 2009). Therefore, induced responses in both the EEG theta and gamma bands show higher activity when previously observed items are correctly recognized compared with the induced responses when novel items are correctly rejected (old/new effect) during information retrieval periods (Osipova et al. 2006).

EEG theta activity in the frontal regions is higher during the encoding of a stimulus that has been retrieved in association with contextual information than during encoding of a stimulus that was remembered without the associated contextual information. Moreover, an increase in the mid-frontal theta power is related to interference processes that are elicited by non-targeted material, which must be overlooked during memory

retrieval tests (Staudigl et al. 2010). In addition, during an incidental object recall test (Gruber et al. 2008), in which figures of objects to be classified as living/non-living or larger/smaller than a shoe box were presented to subjects to be incidentally learned and encoded, EEG gamma band activity was induced by the retrieval of images of objects that had to be recognized as previously seen or not previously seen. Under these conditions, EEG gamma band activity in the parietal-occipital regions was higher during successful recognition (an object correctly classified as previously seen) than during correct rejections (an object correctly classified as new), regardless of the subject's remembering of other specific object's qualities in each test (e.g., remembering the object and the learning/retrieval task in which it was presented (recollection) or remembering the object but not the learning/retrieval task in which it was presented (familiarity)). In addition, the theta (4–7.5 Hz) activity recorded in the fronto-central cortical regions when items were correctly recognized was higher under recollection than under familiarity remembering conditions.

A relationship between theta activity and object-memory tasks has been found to be associated with hippocampal function using fMRI. Here, the activation of the anterior hippocampus, the perirhinal cortex and the anterior parahippocampal cortex has been shown to be related to the perception of novel objects, whereas the posterior hippocampus and the posterior parahippocampal cortex seem to be activated during the processing of novel arrangements of familiar objects (Pihlajamäki et al. 2004; Smith and Milner 1981).

In fact, this is demonstrated using an experimental schedule in which three objects that are randomly placed in a 3 square $\times$ 3 square grid and are visible within 5 $\times$ 5 of the visual field. These three objects are presented to each subject, and the subject tries to learn their positions over 8 s before attempting to place the object in its original arrangement within 30 s. The researchers then analyse the subsequent recall-related EEG. The researchers observed higher theta activity in EEG recordings from fronto-central to posterior regions when the object was correctly placed during recall (Sato and Yamaguchi 2007). Thus, changes in theta and gamma activity are associated with episodic object position memory that was intentionally acquired.

A decline in the quality of memory for spatial information, including deficiencies in the explicit recall of

the locations of objects in a virtual room, can be observed as age increases (Kessels et al. 2005). Furthermore, deficiencies in remembering the positions of objects in a picture have also been observed (Shih et al. 2012). Memory of object location was deficient in older adults when associations between objects and locations were required in the tasks (Kessels et al. 2005) as well as when only contextual information was evaluated (object position, without attending to its identity). Furthermore, a higher deficiency has been observed in spatial information compared to object identity information memory under intentional acquisition conditions (Kessels et al. 2007). Thus, it has been proposed that attentional neural processes could not be required for the encoding of spatial locations (Hasher and Zacks 1979) and that spatial memory could be an automatic process that is slightly altered by ageing.

Nevertheless, various studies have obtained evidence that episodic spatial memory and other modalities of episodic memory decline with age, although the results are highly variable due to methodological differences regarding the experimental schedules, the specificity of the location of items and the intentional or incidental methods for information acquisition (Uttl and Graf 1993). Thus, contrasting incidental versus intentional experimental conditions lead to a differential performance between less efficient old and efficient young subjects in tasks under intentional or incidental conditions. The intentional processing of acquired information in different tasks that assess spatial localization seems to result in better performing support for older adults than for younger adults. Moreover, the specific evaluation of spatial location memory confirmed a marked loss of memory under incidental learning conditions for older adults. In fact, older adults with poor performance while learning spatial locations under incidental learning had better performance under intentional learning and encoding information (Shih et al. 2012).

Thus, it is possible that differences exist in the incidental or intentional coding of visuospatial information between young adults and mature adults in association with different expressions of theta and gamma EEG activities. Therefore, we sought to analyse the characteristics of the theta and gamma bands of EEG recordings in young and mature adults during incidental or intentional behavioural conditions of learning and recalling in a visuospatial task.

Materials and methods

Twenty-six healthy, right-handed men without visual impairment participated in this study. These subjects were allotted to either the young adult group ($n=14$, 18–25 years old) or the mature adult group ($n=12$, 45–65 years old) according to their ages. To exclude participants suffering from depressive or anxiety disorders, the BDI and BAI inventories were used. These inventories have proved to be widely useful in both clinical and community samples, and versions adapted to Spanish language have been validated (Jurado et al. 1998; Manian, Schmidt, Bornstein and Martinez 2013; Robles and Páez 2003). For inclusion in this study, participants had to obtain scores higher than 23 on the Mini Mental State Test (the limit for mild cognitive impairment), lower than 48 in the Beck's depression scale (corresponding to minimal or absent depressive symptoms), lower than 8 in the Beck's anxiety scale (corresponding to minimal or absent behavioural alteration related to anxiety levels) and within the mean normal-normal high range (50–90 % percentile, corresponding to an average or above-average intelligence level) in the dominoes test (Anstey). Participants were also required to have an absence of degenerative brain disorders, stroke or severe head trauma in their clinical history to be included in the study.

The study was approved by the Research and Ethics Committee of the Coordinación de Investigación en Salud, of the Instituto Mexicano del Seguro Social, and by the Research and Ethics Committee of the Facultad de Ciencias Médicas y Biológicas “Dr. Ignacio Chávez”; written informed consent was obtained from each individual included in the study.

EEG recordings

EEGs were recorded during the behavioural task from FZ, F3, F4, F7, F8, FP1, FP2, P3, P4, T5 and T6 monopolar derivations (10/20 electrode placement international system), which were referenced to ear lobes (Nicolet Biomedical Alliance Works EEG Unit). High and low filters were set at 1 and 100 Hz, with an Fm of 128 Hz. EEG recordings were obtained from all subjects under the following conditions: 1 min baseline (open eyes looking at a white sheet that was placed 60–70 cm in front of the face) and throughout the time required to perform each incidental and intentional learning procedure. One-second segments from these EEGs were

processed (EEG Imagine 2.2, Medical Imaging Solutions 2002; Nic Vue 2.5.1 Nicolet Biomedical 2002) by selecting samples through a low 4-Hz/high 45-Hz cutoff filter at a 120-Hz sampling rate. These segments were subjected to fast Fourier transform (FFT) analysis to obtain the absolute power (AP) values of the theta (4–8 Hz) and gamma (30–45 Hz) bands for each behavioural condition (see above) and derivation.

Incidental/intentional visuospatial learning test

After the baseline was recorded while the participants observed a white sheet with a dot in the centre, the EEG was continuously recorded as the visuospatial intentional and incidental learning was evaluated under the following sequential schedule. First, a printed drawing of a maze including figures of six common objects (balloon, cup, butterfly, watch, pine tree and arrow) in specific locations was presented to the participants to be observed for the duration required by each subject to solve the maze by connecting its entrance (table symbol) and exit (flowerpot symbol) points (the subjects tended to ignore the table and flowerpot symbols in the incidental and intentional memory tests) (Fig. 1a). Next, subjects were asked to observe the maze for 1 min without any other instruction (the incidental learning condition in the EEG analysis). Subjects were then asked to solve the task by recalling the correct trajectory through the maze, from the entrance to the exit (distractor task). Next, subjects were asked to remember (without making any movement) the position of the objects in the original maze, without identifying them, on a printed drawing of the maze lacking the objects (the incidental memory condition in the EEG analysis) (Fig. 1b). Subjects were next asked to mark, from memory, the positions of the objects (using X symbols) on a printed drawing of the maze lacking the objects (measure of incidental memory ability). Finally, subjects were allowed to study the position of the objects (the intentional learning condition in the EEG analysis) from the original printed drawing of the maze for 1 min and then asked to mark, from memory, the positions of the objects on a second printed maze lacking the objects (measure of intentional memory ability). Figure 2 presents a schematic of the task.

Three main parameters were obtained from the subjects' performance in these incidental or intentional

Fig. 1 Drawings of the maze with and without the visuospatial signals used for testing incidental and intentional visuospatial learning/memory performance

learning/memory tests: the total number of remembered object positions, the number of correctly remembered positions (positions marked in the exact location of the objects' figures in the maze) and the index error, obtained by summing the lengths (in cm) of the deviations between each correct object position and the corresponding mark placed by the subjects when attempting to identify its position and dividing this value by the total number of remembered positions. Behavioural comparisons between young and mature adults as well as comparisons of the absolute power for each derivation between conditions and between groups (for each derivation and condition) were conducted.

In addition, subjects were classified according to their performance in the incidental learning/memory test, regardless of age. Specifically, we classified the participants and grouped them in a high-performance group ($n=9$), consisting of subjects who correctly remembered at least five of the eight total object positions and correctly placed at least four of these objects in the maze, and a low-performance group ($n=17$), consisting of subjects who did not achieve these performance levels. Similarly, subjects were also classified and divided according to their performance in the intentional learning/memory tests, resulting in a high-performance group ($n=17$), including subjects who correctly

Fig. 2 Diagrammatic representation of the behavioural task

remembered at least five object positions, and a low-performance group ($n=9$), including subjects who correctly remembered four or fewer object positions. Using these classification criteria, the behavioural differences were significant for all parameters of the intentional and incidental tests when statistical comparisons were conducted (data not shown).

Groups of parameters for incidental and intentional learning/memory performance were compared using the t test (error index for both incidental and intentional tests and dominoes efficiency percent) and the Mann-Whitney U test (total number of positions remembered and number of positions correctly remembered, as well as the Beck test scores, years of study and age). The correlations (Pearson) between these behavioural variables and age, years of study and dominoes test scores were also determined.

The comparisons between conditions for each group and between groups and conditions for each derivation were conducted as follows. Power values transformed in the natural logarithm of theta and gamma bands were compared between conditions (ANOVA for blocks and Tukey's test) for each group. Additionally, using ANOVA and Tukey's test, we compared the natural logarithms of the power values of the theta and gamma bands between the age groups and behavioural condition for each derivation. To compare the participants' incidental or intentional memory performance efficiencies, ANCOVA was conducted using age as the covariate to assess whether differences between groups persisted. In addition to ANCOVA, a logistic regression was calculated using performance as a dichotomous dependent variable (high or low) and age and power as independent variables. This regression was conducted to assess the contribution of each of these factors to the differences in the participants' performance in each test.

Results

Table 1 shows the demographic data for the young and mature adult groups. These groups were significantly different in terms of age and dominoes test performance ($p<0.001$). A significant negative correlation between age and efficiency was observed for the dominoes test score ($r=-0.668$, $p<0.001$). There were no differences between groups in terms of either years of study or correlations between years of study and any variable

Table 1 Main demographic data (mean $\pm$ SE) of young adult and mature adult subjects included in the study

	Young adults ($n=14$)	Mature adults ($n=12$)
Age	21.5 $\pm$ 2.53	52.75 $\pm$ 5.59*
Years of study	18.071 $\pm$ 1.49	17.83 $\pm$ 7.23
Mini Mental Test	31.6 $\pm$ 1.90	31.818 $\pm$ 1.25
Domino's test efficiency (percent)	72.2 $\pm$ 7.90	57 $\pm$ 7.45*

*Student's t test, young versus mature adults, $p<0.001$

of the visuospatial incidental or intentional learning/memory tests.

Incidental/intentional visuospatial learning

The young adult group had a significantly higher number of total remembered positions (median=5, 25 % percentile=4; 75 % percentile=6; maximum=6; minimum=4) than the mature adult group (median=4, 25 % percentile=3.25, 75 % percentile=5, maximum=6, minimum=0) during the incidental visuospatial learning test ($\chi=125$, $p=0.027$), but no differences in the number of positions correctly remembered ($\chi=116.5$, $p=0.087$) (young group median=4, 25 % percentile=1.75, 75 % percentile=4, maximum=6, minimum=1; mature adult group median=3, 25 % percentile=1.25, 75 % percentile=3, maximum=4, minimum=0) or the error index (young group mean 1.202 ± 0.311 , mature group mean 1.589 ± 0.328 ; $t=-0.395$, $p=0.697$) were observed between the groups. A significant negative correlation between the total number of remembered positions and age was observed for the incidental test ($r=-0.509$, $p=0.011$) (Fig. 3). In the intentional test, no differences were observed between the groups in terms of the total number of positions remembered (young adults median=6, 25 % percentile=6, 75 % percentile=6, maximum=6, minimum=5; mature adults median=6, 25 % percentile=6, 75 % percentile=5, maximum=6, minimum=5; $\chi=107.0$, $p=0.124$), but differences were observed in the number of positions correctly remembered (young adults median=6, 25 % percentile=5, 75 % percentile=6, maximum=6, minimum=4; mature adults median=4.5, 25 % percentile=3.25, 75 % percentile=5.75, maximum=6, minimum=1; $\chi=132$, $p=0.008$) and the error index (young adults mean 0.2631 ± 0.070 ; mature adults mean 0.5904 ± 0.170 ; $t=-2.208$, $p=0.037$). Specifically, the number

Incidental learning

Fig. 3 Comparisons between age groups in terms of total remembered positions, correctly remembered positions, and error index and graphs of their correlation with age under incidental or intentional learning/memory testing in young and mature adults. * $p < 0.05$

of correctly remembered positions was significantly lower for the mature adult group than for the young

adult group; consequently, the error index was significantly higher for the mature adult group. A significant

Table 2 Inter-group comparison of absolute power values (natural logarithm, mean $\pm$ SE) of EEG theta and low gamma frequency bands, from different frontal temporal and parietal EEG derivations

	Theta (4-8 Hz)			Low Gamma (30-45 Hz)		
	Young Adult	Mature Adult	P	Young Adult	Mature Adult	P
Fp2				<u>2.393 $\pm$ 0.038</u>	<u>2.525 $\pm$ 0.066</u>	0.005
F7	<u>2.494 $\pm$ 0.036</u>	<u>2.299 $\pm$ 0.045</u>	0.001	2.494 $\pm$ 0.036	2.709 $\pm$ 0.071	0.006
F8	<u>2.473 $\pm$ 0.042</u>	<u>2.272 $\pm$ 0.050</u>	<u>0.002</u>	2.473 $\pm$ 0.042	2.688 $\pm$ 0.074	0.011
T3	2.641 $\pm$ 0.062	2.009 $\pm$ 0.040	< 0.001	<u>2.641 $\pm$ 0.062</u>	<u>2.840 $\pm$ 0.058</u>	0.002
T4	2.595 $\pm$ 0.054	1.962 $\pm$ 0.041	< 0.001	2.595 $\pm$ 0.054	2.828 $\pm$ 0.067	0.007
T5	2.702 $\pm$ 0.058	2.035 $\pm$ 0.037	< 0.001			
T6	2.641 $\pm$ 0.057	1.972 $\pm$ 0.034	< 0.001	<u>2.641 $\pm$ 0.057</u>	<u>2.732 $\pm$ 0.065</u>	0.001
P3	2.554 $\pm$ 0.060	2.205 $\pm$ 0.035	< 0.001			
P4	2.556 $\pm$ 0.044	2.177 $\pm$ 0.033	< 0.001			

Only derivations with statistically significant differences are included. ANOVA for two factors (group and behavioural condition). Underlined data were significant in the ANCOVA, for both group and age (double line), only for group (single line) or only for age (segmented line). Grey data were significant only for the ANCOVA

negative correlation between the number of correctly remembered positions and age ($r = -0.599$, $p = 0.002$) as well as a positive correlation between the error index and age ($r = 0.471$, $p = 0.02$) were observed for the intentional test (Fig. 3).

EEG

Young Adults versus Mature Adults

The intergroup comparison of the absolute power in the theta band (4–8 Hz) recorded from the frontal (F7 and F8), temporal (T3, T4, T5 and T6) and parietal (P3 and

P4) recording sites (main effect) revealed significantly lower power values in the mature adult group than in the young adult group. Significant differences were also observed in the low gamma frequency band (30–45 Hz), with the mature adults demonstrating higher absolute power values than the young adults in the frontal (F7 and F8) and temporal (T3 and T4) recording sites. When the age was included as a covariate (ANCOVA), the AP of the theta band only showed significant differences between groups for the F8 derivation and a significant effect of age for the F8 and F7 recording sites. In the gamma band, the AP was significantly higher for the mature adults in T3, T6 and Fp2, and a significant effect of age was observed in T6 and

Fig. 4 Power values (natural logarithms) of EEG theta frequency (4–8 Hz) activity recorded from different electrode placements over the frontal, parietal and temporal cerebral cortical regions

under incidental (*Inc*) and intentional (*Int*) learning/memory testing conditions in young and mature adult subjects. *B* basal, *L* learning, *M* memory. * $p < 0.05$, ANOVA and Tukey's test

Table 3 Comparison of absolute power values (natural logarithm, mean $\pm$ SEM) of EEG theta frequency band activity from different frontal temporal and parietal EEG derivations, between subjects grouped by their efficiency in performing under the incidental learning task

	Theta (4–8 Hz)			Gamma (30–45 Hz)		
	High Performance	Low Performance	P	High Performance	Low Performance	P
F3	<u>2.498 $\pm$ 0.051</u>	<u>2.364 $\pm$ 0.038</u>	0.033			
F4	<u>2.514 $\pm$ 0.069</u>	<u>2.331 $\pm$ 0.036</u>	0.009			
F7	2.548 $\pm$ 0.042	2.327 $\pm$ 0.042	< 0.001	<u>2.644 $\pm$ 0.069</u>	<u>2.566 $\pm$ 0.051</u>	<u>0.037</u>
F8	<u>2.504 $\pm$ 0.053</u>	<u>2.314 $\pm$ 0.041</u>	0.006			
T3	<u>2.682 $\pm$ 0.082</u>	<u>2.173 $\pm$ 0.050</u>	< 0.001	<u>2.804 $\pm$ 0.077</u>	<u>2.695 $\pm$ 0.053</u>	<u>0.058</u>
T4	<u>2.641 $\pm$ 0.061</u>	<u>2.124 $\pm$ 0.051</u>	< 0.001			
T5	<u>2.731 $\pm$ 0.076</u>	<u>2.216 $\pm$ 0.050</u>	< 0.001			
T6	<u>2.583 $\pm$ 0.081</u>	<u>2.200 $\pm$ 0.052</u>	< 0.001			
P3	<u>2.565 $\pm$ 0.076</u>	<u>2.302 $\pm$ 0.042</u>	0.001			
P4	<u>2.553 $\pm$ 0.059</u>	<u>2.291 $\pm$ 0.051</u>	< 0.001			

Only derivations with statistically significant differences are included. *P* values correspond to the ANOVA for two factors (group and behavioural condition). Data were significant in the ANCOVA, for both group and age (italics) or only for age (bold italics). Gray data were significant only for the ANCOVA

FP2 (Table 2). No differences were observed in the age and behavioural condition interactions.

Analysis of the theta band of the absolute power of EEG activity recorded from each electrode placement under each behavioural condition of the young group revealed a significant difference only in the Fp2 derivation [$F(3,39)=6.752$, $p=0.001$], where the power was higher ($p=0.033$) in the intentional learning condition than in the basal recording (Fig. 4). However, in the mature adult group, the values of theta band absolute power during the incidental memory and intentional learning conditions were higher in the frontal and parietal recording sites Fp1 [$F(3,33)=9.740$, $p<0.001$; $p=0.002$ and $p=0.001$, respectively], Fp2 [$F(3,33)=10.658$, $p<0.001$; $p=0.001$ and $p=0.002$, respectively], F3 [$F(3,33)=6.845$, $p=0.001$; $p=0.030$ and $p=0.043$, respectively] and Fz [$F(3,28)=9.948$, $p<0.001$; $p<0.001$ and $p=0.001$, respectively] than in the basal condition. The absolute theta band power in F4 was only higher than the basal condition under the incidental memory condition [$F(3,33)=7.126$, $p=0.001$; $p=0.020$], whereas the absolute theta band power was higher during the intentional learning stage

than in the basal condition in T4 [$F(3,33)=4.937$, $p=0.006$; $p=0.052$], T6 [$F(3,33)=9.604$, $p<0.001$; $p=0.011$], P3 [$F(3,33)=13.964$, $p<0.001$; $p=0.035$] and P4 [$F(3,33)=11.201$, $p<0.001$; $p=0.035$] (Fig. 3). Finally, the power in FZ was also higher under the incidental learning condition compared to the basal condition in the mature adult group ($p<0.01$) (Fig. 4).

Incidental Learning in High-Performance Subjects versus Low-Performance Subjects

Intergroup comparisons between subjects with high performance ($n=9$) and subjects with low performance ($n=17$) in the incidental learning tasks showed significant differences in the frontal, temporal and parietal recording sites. The ANOVA results revealed that the absolute power values of the theta band were significantly lower in the low-performance group in F3 [$F(1,96)=4.690$, $p=0.033$], F4 [$F(1,96)=7.163$, $p=0.009$], F7 [$F(1,96)=15.094$, $p<0.001$], F8 [$F(1,96)=7.925$, $p=0.006$], T3 [$F(1,96)=31.755$, $p<0.001$], T4 [$F(1,96)=39.038$, $p<0.001$], T5 [$F(1,96)=33.655$, $p<0.001$], T6 [$F(1,96)=17.139$,

$p < 0.001$], P3 [$F(1,96) = 12.212$, $p = 0.001$] and P4 [$F(1,96) = 16.658$, $p < 0.001$] than in the high-performance group. However, ANCOVA only showed group significant differences for P3, whereas a significant effect of age was evident for all aforementioned recording sites (Table 3). ANOVA did not reveal significant differences in the absolute power values of the low-gamma EEG activity and did not show significant differences between the high- and low-performing subjects in the incidental learning tasks. However, ANCOVA using age as the covariate indicated significant differences between groups for F7 and a tendency for T3 to have higher power in the high-performance group.

No differences were observed in the absolute power of EEG theta activity between the basal condition and any other learning/memory condition in the high-performance group; however, significant differences were observed in the EEG theta band absolute power

values between the basal and incidental memory conditions and between the basal and intentional learning conditions in the low-performance group. Specifically, the absolute power values were higher under the incidental and intentional memory conditions than under the basal condition in Fp1 [$F(3,48) = 7.965$, $p < 0.001$; $p = 0.011$ and $p = 0.018$, respectively], Fp2 [$F(3,48) = 11.402$, $p < 0.001$; $p = 0.001$ and $p = 0.001$, respectively], Fz [$F(3,43) = 9.491$, $p = 9.491$, $p < 0.001$; $p = 0.008$ and $p = 0.049$, respectively] and P3 [$F(3,48) = 12.380$, $p < 0.001$; $p = 0.016$ and $p = 0.004$, respectively]. Additionally, in P3, the theta band absolute power values during the incidental learning condition were lower than those during the intentional learning condition (0.044) (Fig. 5). We also observed an elevated power in F3 during the intentional learning condition compared with the basal condition [$F(3,48) = 7.853$,

Fig. 5 Power values (natural logarithms) of EEG theta frequency (4–8 Hz) activity recorded from different electrode placements over the frontal, parietal and temporal cerebral cortical regions in

high- and low-performance subjects under incidental (*Inc*) and intentional (*Int*) learning/memory testing conditions. B basal, L learning, M memory. * $p < 0.05$, ANOVA and Tukey's test

$p < 0.001$; $p = 0.024$], F7 [$F(3,48) = 4.230$, $p = 0.010$; $p = 0.049$] and P4 [$F(3,48) = 14.661$, $p < 0.001$; $p = 0.020$] (Fig. 5, Table 3).

Logistic regression analysis using age and theta power as independent variables and performance (low and high) as the dependent variable indicated that the age had a significant influence on performance. However, no significant relationship between theta power and performance was found, with only a tendency for P3 (0.051) and T4 (0.060). Gamma band power was significantly related to performance only for F7, whereas age was significant for all recording sites (Table 4).

Intentional Learning in High-Performance Subjects versus Low-Performance Subjects

Significant intergroup differences between the high- and low-performance groups were found in the absolute theta power values during task solving in the intentional learning tasks. ANOVA revealed that these values were significantly higher in the high-performance group than in the low-performance group at the frontal (F3, F4, F7, F8), parietal (P3 and P4) and temporal (T3, T4, T5 and T6) sites (Table 5). Additionally, intergroup differences in the gamma power values were observed in the frontal

Table 4 Logistic regression for the performance (dependent variable) in the incidental test considering age and absolute power (ln) of the theta or gamma bands (independent variables)

	Age				Power			
	Cte.	OR	CI 95 %	<i>p</i> value	Cte.	OR	CI 95 %	<i>p</i> value
Theta								
Fp1	0.086	1.089	0.047–0.126	0.000	0.407	1.52	−1.627–2.442	0.695
Fp2	0.085	1.008	0.046–0.124	0.000	0.208	1.231	−1.712–2.128	0.832
Fz	0.078	1.081	0.039–0.116	0.000	−0.355	0.701	−1.686–0.976	0.601
F3	0.094	1.098	0.051–0.137	0.000	1.142	3.133	−1.000–3.284	0.296
F4	0.096	1.100	0.052–0.140	0.000	1.332	3.788	−0.968–3.632	0.256
F7	0.083	1.086	0.046–0.120	0.000	−0.453	0.010	−2.499–1.593	6.664
F8	0.083	1.086	0.046–0.121	0.000	−0.198	0.820	−1.895–1.499	0.819
P3	0.108	1.114	0.061–0.154	0.000	2.000	7.389	−0.010–0.411	0.051
P4	0.081	1.084	0.040–0.123	0.000	−0.381	0.683	−3.075–2.312	0.781
T3	0.086	1.089	0.047–0.126	0.000	0.344	1.410	−1.881–2.569	0.762
T4	0.077	1.080	0.039–0.115	0.000	−2.161	0.115	−4.417–0.095	0.060
T5	0.078	1.081	0.039–0.117	0.000	−0.997	0.368	−3.698–1.704	0.469
T6	0.082	1.085	0.044–0.119	0.000	−0.677	0.508	−3.329–1.975	0.617
GAMMA								
Fp1	0.143	1.153	0.059–0.227	0.000	−0.013	0.987	−1.188–1.162	0.983
Fp2	0.140	1.150	0.056–0.225	0.000	0.358	1.430	−0.913–1.628	0.581
Fz	0.124	1.132	0.038–0.209	0.000	0.174	1.190	−1.087–1.434	0.787
F3	0.162	1.175	0.072–0.253	0.000	−0.958	0.383	−2.165–0.249	0.120
F4	0.148	1.159	0.062–0.234	0.000	−0.306	0.736	−1.319–0.706	0.553
F7	0.198	1.218	0.092–0.305	0.000	−1.581	0.205	−2.984–−0.178	0.027
F8	0.164	1.178	0.071–0.258	0.000	−0.790	0.453	−1.956–0.375	0.184
P3	0.148	1.159	0.062–0.233	0.000	−0.531	0.588	−1.625–0.562	0.341
P4	0.146	1.157	0.061–0.231	0.000	−0.446	0.640	−1.803–0.911	0.519
T3	0.165	1.179	0.074–0.255	0.000	−1.022	0.359	−2.103–0.060	0.064
T4	0.174	1.190	0.078–0.270	0.000	−0.898	0.407	−2.055–0.259	0.128
T5	0.152	1.164	0.066–0.238	0.000	−0.837	0.443	−1.938–0.263	0.136
T6	0.142	1.152	0.058–0.226	0.000	0.161	1.174	−0.859–1.181	0.757

bold *p* values were significant

Table 5 Comparison of absolute power values (natural logarithm, mean $\pm$ SEM) of EEG theta and gamma frequency band activity from different frontal temporal and parietal EEG derivations, between subjects grouped by their efficiency in performing under the intentional learning task

	Theta (4–8 Hz)			Low Gamma (30–45 Hz)		
	High Performance	Low Performance	P	High Performance	Low Performance	P
Fz				<u>2.471 $\pm$ 0.046</u>	<u>2.207 $\pm$ 0.047</u>	0.001
F3	<u>2.476 $\pm$ 0.040</u>	<u>2.228 $\pm$ 0.043</u>	0.002	<u>2.595 $\pm$ 0.048</u>	<u>2.374 $\pm$ 0.058</u>	0.006
F4	<u>2.470 $\pm$ 0.046</u>	<u>2.252 $\pm$ 0.041</u>	0.002	<u>2.588 $\pm$ 0.058</u>	<u>2.392 $\pm$ 0.053</u>	0.030
F7	2.471 $\pm$ 0.036	2.277 $\pm$ 0.047	0.001	<u>2.638 $\pm$ 0.048</u>	<u>2.507 $\pm$ 0.067</u>	<0.001
F8	<u>2.468 $\pm$ 0.038</u>	<u>2.214 $\pm$ 0.057</u>	<0.001	<u>2.616 $\pm$ 0.049</u>	<u>2.488 $\pm$ 0.080</u>	0.001
P3	<u>2.477 $\pm$ 0.050</u>	<u>2.235 $\pm$ 0.059</u>	0.002	<u>2.628 $\pm$ 0.048</u>	<u>2.474 $\pm$ 0.062</u>	0.039
P4	<u>2.464 $\pm$ 0.043</u>	<u>2.226 $\pm$ 0.043</u>	<0.001	<u>2.613 $\pm$ 0.043</u>	<u>2.515 $\pm$ 0.040</u>	0.009
T3	<u>2.504 $\pm$ 0.063</u>	<u>2.057 $\pm$ 0.050</u>	<0.001	<u>2.782 $\pm$ 0.053</u>	<u>2.640 $\pm$ 0.076</u>	0.004
T4	<u>2.462 $\pm$ 0.057</u>	<u>2.003 $\pm$ 0.052</u>	<0.001	<u>2.711 $\pm$ 0.051</u>	<u>2.686 $\pm$ 0.083</u>	0.002
T5	<u>2.546 (0.062)</u>	<u>2.108 (0.050)</u>	<0.001	<u>2.770 $\pm$ 0.049</u>	<u>2.643 $\pm$ 0.067</u>	0.013
T6	<u>2.438 (0.056)</u>	<u>2.133 (0.077)</u>	0.002			

Only derivations with statistically significant differences are included. Black P values correspond to the ANOVA for two factors (group and behavioural condition) grey P values correspond to the ANCOVA (when data were only significant in the ANCOVA). Underlined data were significant in the ANCOVA, for both group and age (double line), only for group (single line) or only for age (segmented line)

(Fz, F3, F4) and parietal (P3) recordings, in which the absolute gamma power values were lower in the low-performance group than in the high-performance group (Table 5). However, ANCOVA of the theta AP revealed significant differences by group in the F8 and T3 derivations, whereas significant effects of age were found in all aforementioned recording sites. In the gamma band, significant effects of group and age were observed in the ANCOVAs for all the sites that were significant for the ANOVAs and for additional sites (F7, F8, P4, T3 and T4), and only for the T5 site was a group effect found (Tables 5 and 6).

The absolute theta power values were compared between the different learning conditions for the high-performance and low-performance groups individually. The high-performance group had theta power values higher than in Fz [$F(3,48)=7.696$, $p<0.001$] theta during intentional learning relative to the basal condition (0.026) which were observed for the high-performance group. The absolute theta power values of the low-performance group showed changes in the frontal and parietal, but not temporal, derivations under the different

learning conditions. Thus, the recordings from Fp1 [$F(3,24)=10.745$, $p<0.001$], Fp2 [$F(3,24)=13.833$, $p<0.001$], Fz [$F(3,19)=6.616$, $p=0.003$] and P3 [$F(3,24)=8.269$, $p=0.001$] had higher theta power values during incidental memory ($p=0.012$ /Fp1, $p=0.007$ /Fp2, $p=0.027$ /Fz, $p=0.033$ /P3) and intentional learning ($p=0.004$ /Fp1, $p=0.001$ /Fp2, $p=0.012$ /Fz, $p=0.005$ /P3) than in the basal condition. Meanwhile, recordings from F3 [$F(3,24)=16.503$, $p<0.001$], F4 [$F(3,24)=19.772$, $p<0.001$], F7 [$F(3,24)=3.971$, $p=0.020$], F8 [$F(3,24)=7.344$, $p=0.001$] and P4 [$F(3,24)=11.012$, $p<0.001$] showed higher theta power values during the intentional learning condition than during the basal condition ($p=0.015$ /F3, $p=0.011$ /F4, $p=0.049$ /F7, $p=0.047$ /F8, 0.041/P4) (Fig. 6).

The absolute power values of the low gamma band showed differences between behavioural conditions only in the young adult group, being higher in P3 [$F(3,39)=11.951$, $p<0.001$] during the intentional learning condition than in the basal recording ($p=0.033$). No differences in the absolute power values of the low gamma band between learning conditions

Table 6 Logistic regression for the performance in the intentional test (dependent variable) considering age and AP of the theta or gamma bands as independent variables

Theta	Age				Power			
	Cte.	OR	CI 95 %	<i>p</i> value	Cte.	OR	CI 95 %	<i>p</i> value
Fp1	0.064	1.067	0.034–0.095	0.000	−0.091	0.913	−1.695–1.513	1.513
Fp2	0.064	1.066	0.034–0.094	0.000	−0.176	0.838	−1.736–1.410	0.828
Fz	0.057	1.059	0.025–0.089	0.000	−0.069	0.934	−1.486–1.349	0.924
F3	0.060	1.062	0.029–0.092	0.000	−0.681	0.506	−2.355–0.993	0.425
F4	0.058	1.060	0.026–0.090	0.000	−0.941	0.390	−2.725–0.843	0.301
F7	0.064	1.066	0.034–0.094	0.000	−0.353	0.702	−2.057–1.351	0.684
F8	0.058	1.060	0.028–0.088	0.000	−1.787	0.168	−3.430–−0.143	0.033
P3	0.091	1.095	0.053–0.128	0.000	2.153	8.614	0.402–3.905	0.016
P4	0.066	1.068	0.033–0.099	0.000	0.155	1.168	−2.057–2.367	0.891
T3	0.066	1.068	0.035–0.097	0.000	0.196	1.217	−1.638–2.031	0.834
T4	0.060	1.062	0.029–3.189	0.000	−0.856	0.425	−2.731–1.018	0.371
T5	0.063	1.065	0.032–0.093	0.000	−0.464	0.629	−2.489–1.562	0.654
T6	0.061	1.063	0.031–0.092	0.000	−0.974	0.378	−3.202–1.255	0.392
GAMMA								
Fp1	0.227	1.255	0.127–0.327	0.000	−1.665	0.189	−2.933–−0.398	0.010
Fp2	0.225	1.252	0.127–0.323	0.000	−1.331	0.264	−2.575–−0.086	0.036
Fz	0.205	1.227	0.101–0.308	0.000	−3.273	0.038	−5.182–−1.365	0.001
F3	0.266	1.304	0.057–0.374	0.000	−2.774	0.062	−4.247–−1.301	0.000
F4	0.244	1.277	0.142–0.346	0.000	−2.137	0.118	−3.498–−0.755	0.002
F7	0.299	1.349	0.179–0.419	0.000	−2.895	0.055	−4.496–−1.295	0.000
F8	0.263	1.300	0.154–0.371	0.000	−1.975	0.139	−3.246–−0.705	0.002
P3	0.232	1.261	0.130–0.333	0.000	−1.905	0.149	−3.277–−0.534	0.006
P4	0.223	1.250	0.125–0.321	0.000	−1.893	0.151	−3.477–−0.310	0.019
T3	0.259	1.296	0.148–0.370	0.000	−1.829	0.161	−3.103–−0.555	0.005
T4	0.277	1.320	0.162–0.393	0.000	−1.953	0.142	−3.314–−0.593	0.005
T5	0.224	1.251	0.125–0.323	0.000	−1.541	0.214	−2.835–−0.247	0.020
T6	0.205	1.228	0.112–0.298	0.000	−0.368	0.692	−1.419–0.683	0.492

bold *p* values were significant

were recorded in the mature adults. Comparisons of the gamma band absolute power values did not show significant differences across learning conditions in the high-performance group, while the low-performance group showed differences in P3 [$F(3,48)=11.006$, $p<0.001$] and P4 [$F(3,48)=9.711$, $p<0.001$]. Paired comparisons indicated higher gamma band absolute power values during incidental memory ($p=0.005$) and intentional learning ($p=0.008$) than in the basal condition in P3. Meanwhile, in P4, the gamma power was higher during intentional learning compared with either the basal (0.023) or incidental learning (0.038) conditions (Fig. 7). The high-performance adult group

showed differences in the gamma band absolute power values only in recordings from P4 [$F(3,48)=12.700$, $p<0.001$]. Here, the power values during intentional learning were higher than those during the basal condition ($p=0.044$). Meanwhile, in the low-performance group, the gamma power values in P3 were higher [$F(3,24)=5.549$, $p=0.005$] under the incidental memory (0.024) and the intentional learning (0.034) conditions than during the basal condition (Fig. 7).

Logistic regression analysis using the performance level of the subjects in the intentional test as the dependent variable (low and high performance) and theta or gamma power and age as the independent variables

Fig. 6 Power values (natural logarithms) of EEG theta frequency (4–8 Hz) activity recorded from different electrode placements over the frontal, parietal and temporal cerebral cortical regions in

showed that the theta power significantly contributed to the differences in performance only in the F8 and P3 derivations, whereas age is significantly related to performance for all the recording sites. However, in the gamma band, both age and AP were significant in all derivations except T6, in which only age contributed to the performance differences (Table 6).

Discussion

The results from the present work show a significant difference in performance under incidental learning conditions between the mature adult group (averaging

high- and low-intentional-performance subjects under incidental (*Inc*) and intentional (*Int*) learning/memory testing conditions. *B* basal, *L* learning, *M* memory. * $p < 0.05$, ANOVA and Tukey's test

52.75 years old) and the young adult group (averaging 21.5 years old). We also demonstrated a significantly negative correlation between the parameters of individual incidental (total number of remembered or number of correctly remembered figure positions) or intentional learning performance and age. Indeed, mature adults demonstrated a lower capacity to remember than did young adults, although information recall accuracy was preserved under the incidental visuospatial learning/memory conditions. Meanwhile, recall accuracy was significantly diminished when mature adults performed intentional visuospatial learning/memory tasks. In this way, Uttil and Graf (1993) demonstrated that incidental learning is more vulnerable to ageing

Fig. 7 Power values (natural logarithms) of EEG gamma frequency (30–45 Hz) activity recorded from different electrode placements over parietal cerebral cortical regions, under incidental (*Inc*) and intentional (*Int*) learning/memory testing conditions, in young

and mature adult subjects (*upper graphs*). Values of the same parameter in low and high, incidental and intentional performing subjects (*lower graphs*); *B* basal, *L* learning, *M* memory. * $p < 0.05$, ANOVA and Tukey's test

than intentional learning is. Additionally, the incidental recall of pictures and symbols was negatively correlated with age in 72–95-year-old subjects (Bryan and Luszcz 2000). Accordingly, cognitive processes, such as incidental learning/memory, are affected relatively early during ageing (Moscovitch and Winocur 1995). This may be related to functional alterations in the prefrontal cortex, including frontal cerebral regions that indicate age-dependent hypometabolism (Oosterman et al. 2004), which may be associated with cognitive decline.

These results highlight the vulnerability of visuospatial learning abilities, as indicated by the general decline in these skills, in mature adults; however, this decline exhibits different characteristics under incidental and intentional conditions. Accordingly, the present work provides relevant data regarding the differential qualities in performing two learning processes with similar

information content but different intentionality, which supports the differential codification of information under incidental or intentional learning/memory requirements.

Several experimental datasets have supported the relevance of theta activity as an electrophysiological correlate for the adequate codification of information during spatial learning/memory trials (Olvera-Cortes et al. 2002; Olvera-Cortes et al. 2004). In fact, high values of the absolute or relative power of hippocampal or prefrontal EEG theta activity, which is recorded during different steps of spatial learning and memory tasks, are correlated with the higher efficiency in learning and retrieval of information in young male rats relative to old male rats (Olvera-Cortes et al. 2012).

In humans, the subsequent memory effect has been consistently observed in verbal memory tasks as a higher power of theta activity or higher coherence

between regions for EEG activity in the theta range during the encoding of information (Klimesch et al. 1996; Weiss et al. 2000; Weiss and Rappelsberger 2000). Additionally, because a spatial dimension is essential for episodic memory, some studies have shown changes in the power and coherence of the EEG theta band during visuospatial learning in the central and posterior frontal regions. In fact, higher EEG theta power and coherence, predominantly in the 7.0–7.5-Hz frequency range, have been observed under intentional object position associations (Sato and Yamaguchi 2007) as well as under higher evoked potentials during object context associations (Mecklinger and Muller 1996). Nevertheless, EEG correlates of incidental visuospatial learning have rarely been studied.

The lower values of EEG theta band power recordings from the frontal, temporal and parietal regions in mature adults could be related to ageing. When comparing the data including age as a covariate, significant differences between groups were persistent only in F8; thus, F8 is probably reflecting differences between AP values related to performance, whereas all the other differences are explained by age-related changes.

A decrease in the power of theta activity and an increase in rapid activity have been observed in ageing healthy subjects between 30 and 80 years of age based on changes in the EEG spectral characteristics evaluated at different ages (Duffy et al. 1993). Accordingly, in the present work, the mature healthy adults showed generally lower absolute theta power values, mainly due to low theta power values, under basal and incidental learning conditions (comparisons not shown). Also, mature adults exhibited higher absolute gamma power values in the frontal (F7 and F8) and temporal (T3 and T4) regions than did young adults. When age was included as a covariate, differences remained in T3, and differences were also observed for T6 and Fp2.

Differences in basal/incidental learning between groups were observed in all EEG derivations (data not shown). These results support the idea of a general reduction of theta power under basal activity/incidental learning, which could be related to the deficient behavioural performance of mature adults. These data suggest that the activation of brain processes required for both incidental learning/memory and intentional learning in mature adults can be related to high levels of theta activity. This finding is similar to observations in young adults under basal conditions. In fact, it has been shown that better performance in a three-back verbal working

memory task is related to higher theta activity recorded under basal conditions (Heister et al. 2013). Thus, the increase of these low levels of theta activity under incidental memory and intentional learning observed in mature adults under basal and incidental learning could be an EEG correlate of neural processes that account for the mature adults' performance under incidental memory and intentional learning conditions.

It is apparent from the present results that the absolute theta power exhibits differential characteristics in young and mature adults during the performance of incidental or intentional learning/memory tasks. This is possibly related to the different requirements of intentional mental effort. In fact, the mature adult group had higher theta power values in the frontal, temporal and parietal regions under the incidental memory and intentional learning conditions. It can be assumed that these tasks require high levels of intentional mental effort. Meanwhile, in the young adult group, an increase in the theta power relative to the basal condition was only observed under intentional learning in Fp2.

These differences could be due to the lower theta activity power under basal conditions in the mature adult group, which could increase concomitantly with the mental intentional effort required to perform the learning/memory tasks. Meanwhile, the young adults appear to be able to sustain their high performance during a high expression of theta activity power, although additional mental intentional effort might not be required to perform the task under the learning/memory incidental or intentional conditions.

It has been proposed that incidental learning occurs under any attempt to strategically encode information during an on-going activity. Namely, this encoded information is mainly related to the strategies involved in memory retrieval, thereby leading to successful recall in learning/memory tasks, which require efficient retrieval processes (Luszc 1998; Luszc et al. 1997). Therefore, it appears that the power values of EEG theta and gamma activities do not provide electrographic correlates of incidental learning processes, as changes in these parameters were not observed during the incidental encoding of visuospatial information in both young and mature adult groups in the present work. Nevertheless, an increase in EEG theta synchronization and absolute theta power has been observed during the incidental acquisition of words that were being remembered compared to those that were not remembered

(subsequent memory effect) in young subjects (Klimesch 1999; Klimesch et al. 1996). Similar phenomena have been observed by magnetoencephalography techniques in the central, parietal and temporal regions, which are related to remembered or not remembered associations that are incidentally acquired (Staudigl and Hanslmayr 2013). This also occurred under intentional learning conditions during a recognition task (Klimesch et al. 1997a; Klimesch et al. 1997b) when the frequency bands were individually adjusted and the EEG signals from all of the recording sites were averaged.

Conversely, in the present work, the EEG theta and gamma power expression from the different recording sites in young subjects did not show differences under incidental learning when these recording sites were individually analysed to identify a possible differential involvement of cerebral regions under the incidental or intentional tests. Nevertheless, in addition to EEG expressions of theta and gamma power changes, whether other electrographic expressions (as coherence and correlation between the cortical sites) of functional relations between cerebral regions could underlie the level of efficiency of the young and mature groups remains to be evaluated.

However, subjects who had a low performance level in the incidental learning tasks (low-performance group), regardless of age, also showed significantly lower theta power values in the frontal regions (F3, F4) than did subjects with a high performance level (high-performance group). However, when age was included as a covariate, differences by group were only observed for P3, and the logistic regression comparisons showed that age accounted for the performance level in all regions and that T4 and P3 power significantly contributed to explaining the performance. Similarly, differences in theta power were observed in the intentional learning test, and when age was included as a covariate, only F8 and P3 remained significantly different, supporting the relationship between the power in these regions and the different performance levels; the logistic regression showed a significant contribution to the performance in these same recording sites, whereas age was significant for all derivations. Importantly, in addition to the global effect of age, performance level in the incidental test was related to differences in the power of P3, whereas differences in performance in the intentional tests were related to power differences in both P3 and F8.

Gamma activity also showed differential expression related to performance level when age was included as a covariate; differences between high and low performance in the incidental test remained in T3 and F7, and the logistic regression showed a significant contribution of the AP of these two recording sites to performance level. Thus, during incidental learning, the gamma AP in these two regions could be related with the performance level, whereas age was also significant in explaining the performance level. During the intentional test, all recording sites were significant when age was considered as a covariate, and the logistic regressions were significant for all recording sites except the T6 derivation. Thus, under intentional conditions, gamma activity was higher for all recording sites except T6 in the high-performance group and both age and AP explained the performance level. Therefore, higher gamma activity was related with not only mature age but also high performance and was predominant under the intentional learning condition. To this end, higher theta band power in the right frontal cortex and higher gamma band power in the parietal-occipital regions have been reported during the encoding of visual stimuli that were subsequently remembered relative to those recorded during the encoding of not-remembered visual stimuli. This supports the interactive participation of the frontal-posterior cortical regions in coding visual memory (Fries et al. 2013). Furthermore, higher gamma activity has been observed during the mental manipulation (mental change of two characteristics) of visual stimuli, particularly in the frontal and parietal regions, whereas frontal theta activity was enhanced during both the manipulation and maintenance of the memory of the manipulated visual representation (Kawasaki and Watanabe 2007).

Thus, the results of our study may support a relationship between gamma activity and theta/gamma interactions during incidental visuospatial learning. Accordingly, greater gamma activity has been found during recollection (clear and conscious remembering of data containing contextual information) but not during familiarity recognition (perception of familiarity without clear consciousness of the episode in which the information was acquired) in a verbal recognition test in healthy subjects. This data recollection may induce an increased functional connectivity between the frontal and parietal regions, as evidenced by the EEG gamma band characteristics (Burgess and Ali 2002). Frontal and parietal regions, as components of the dorsal

attentional network, have been related to attention (Corbetta et al. 2000; Corbetta and Shulman 2002) and to the establishment of visual episodic memory (Uncapher et al. 2011) in IFMR studies. Although the number of participants in this study is small, the use of ANCOVA and logistic regressions supports our results. In addition, the statistical power was calculated for the size of the sample of participants employed in our study for theta and gamma power comparisons. For theta power, Fz has the lowest statistical power (70 %), P3 has a statistical power of 82 %, and all other derivations have statistical powers of up to 90 %. In the gamma power comparisons, the statistical power was up to 90 %. The calculations were conducted considering a size of effect of 0.3 for gamma and 0.4 for theta AP. In the behavioural comparisons, the statistical power (calculated considering a size of the difference of 1 for the number of positions and 0.3 for the error index) was low for the incidental task (87, 50 and 50 % for total object positions remembered, correct object positions remembered and index error, respectively) and high for the intentional test (99, 97 and 93 % for total object positions remembered, correct object positions remembered and index error, respectively). Thus, a limitation of our study is its low potency to show differences in the incidental test. The lack of differences between young and mature groups in the number of correct positions of objects remembered and index error could be due to the reduced number of participants.

The present study indicates that a reduction of the temporal (T4) and parietal (P3) theta and frontal-temporal (F7, T3) gamma activities was related to poor incidental visuospatial memory performance, whereas a reduction of frontal (F8) and parietal (P3) theta and general reduction of gamma activities were related to low efficiency for intentional visuospatial memory in adults. However, age was related to a general power reduction in both theta and gamma bands; this last finding could be related to a reduction in attentional resources in low-performance individuals. F7 and F8 correspond to the Brodman 45 and 46 areas (inferior frontal gyrus), P3 and P4 correspond to the Brodman 7 area (parietal superior lobule) and T3 and T4 correspond to the Brodman 21 and 22 areas, respectively (temporal middle and superior gyrus) (Homan, Herman and Purdy 1987). Greater activation in young adults relative to older adults was reported in structures such as the frontal superior and inferior bilateral gyrus, right superior temporal gyrus and left supramarginal gyrus in an fMRI

study when the participants judged the familiarity of melodies, although no differences were observed in the ability of the groups (Sikka, Cuddy, Johnsrude and Vanstone 2015). Moreover, age-related alterations in the activation of these structures have been reported in fMRI studies in normal ageing or in mild cognitive impairment (Meinzer et al. 2012; Zhao et al. 2014). Reduced theta activity during automatic encoding of face-place associations reinforced with semantic relatedness was also observed in the left frontal inferior gyrus in association with poor performance in adults aged 59–72 years (Crespo-Garcia, Cantero and Atienza 2012). The present work found a similar effect in adults under 60 years of age (45 to 60 years old except for one 65-year-old subject) as well as marked differences in gamma low AP related to both age and level of performance in incidental (F7 and T3) and intentional (all recorded regions) visuospatial tasks.

Meanwhile, higher gamma power in the frontal and temporal regions appears to be related to ageing but not performance in the same task. Thus, higher EEG theta and gamma activities, which may be involved in brain processes that underlie the encoding of visuospatial information, in young healthy volunteers, have not been supported by the results of the present study. However, in other studies, effects on theta activity were observed when grouping a number of electrodes in a grand mean, not in discrete recording sites. Thus, inefficient performance under incidental or intentional visuospatial learning/memory conditions was associated with a reduction of the frontal, parietal and temporal-temporal theta and gamma power. In addition, in the present study, the deficient intentional and incidental visuospatial learning performances observed in mature adults compared to young adults support a hypothesis of increasing vulnerability of learning abilities during ageing, which can be earlier in the case of visuospatial incidental/intentional tasks than that reported for other classes of information and could be much more profound in subjects older than 60.

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