

Effects of incidental and intentional feature binding on recognition: a behavioural and PET activation study

Lekeu F⁽¹⁾, Marczewski P⁽³⁾, Van der Linden M⁽³⁾⁽⁴⁾, Collette F⁽³⁾, Degueldre C⁽¹⁾, Del Fiore G⁽¹⁾, Luxen A⁽¹⁾, Franck G⁽¹⁾⁽²⁾, Moonen G⁽¹⁾⁽²⁾, Salmon E⁽¹⁾⁽²⁾

⁽¹⁾ *Centre de Recherches du Cyclotron, 8 Allée du 6 Aout-B 30, University of Liège, Sart-Tilman, B-4000 Liège, Belgium*

⁽²⁾ *Department of Neurology, CHU Liège, Belgium*

⁽³⁾ *Department of Neuropsychology, University of Liège, Liège, Belgium*

⁽⁴⁾ *Cognitive Psychopathology Unit, University of Geneva, Geneva, Switzerland*

Abstract

Using Positron Emission Tomography (PET), we investigated cerebral regions associated with the episodic recognition of words alone and words bound to contextual colours. Two modes of colour encoding were tested: *incidental* and *intentional* word-to-colour binding. Word-only recognition was associated with brain activation in a lexico-semantic left middle temporal region and in the cerebellum following an *incidental* colour encoding, and with brain activation in the left posterior middle frontal gyrus, right anterior cingulate and right inferior frontal gyrus following an *intentional* encoding. Recognition of bound features was associated with activation in left prefrontal and superior parietal regions following an *incidental* colour encoding, and with preferential right prefrontal cortex activation following an *intentional* colour encoding. Our results are in line with the hypothesis of a parietal involvement in context processing, and prefrontal areas in monitoring retrieval processes. Our results also support the hypothesis of a 'cortical asymmetry for reflective activity' (CARA).

Keywords: PET; Episodic memory; Context; Colour

1. Introduction

Episodic memory allows to encode, store and retrieve memories of personal events [62]. It relies on the ability to bind central information (e.g. the content of a conversation) to contextual information specific to the event. Contextual information includes temporo-spatial features of the event (the moment and the place of its presentation) but also the modality of encoding (e.g. visual, auditive, ...), physical characteristics such as voice or colour, cognitive operations performed during the event, or emotional state. They may later serve as cues to help retrieving the central information. In the process of creating a coherent memory trace for a particular event, encoding the central information and the context independently is not sufficient. Establishing a link between central and contextual features (*binding* them together), is a crucial operation, necessary to give the memory of an event its specificity and its distinctiveness. The ability to retrieve the memory of an event may depend on the quantity and the strength of associations created between central and contextual information, which places binding processes at the top of the list of fundamental episodic memory operations.

Hasher and Zacks [25] proposed a distinction between automatic and voluntary processing of information. This distinction was echoed in the literature and it was repeatedly postulated that some contextual informations (e.g. spatial context or frequency of occurrence) are best processed automatically (e.g. incidentally), while other contextual informations are processed in an effortful mode (e.g. colours). This assumption does not mean that spatial contextual information cannot be encoded intentionally and colour cannot be encoded incidentally, but rather that the memory for the association between a central piece of information and its context benefits more from one mode of encoding than from the other. Firstly, different studies have brought to light the automaticity of frequency of occurrence [64] or spatial context processing [1,17], though others have observed challenging results [44,45]. Briefly, concerning this challenge, the former study showed no effect of intention or age-

differences on the ability to recall or recognise the contextual information, while the latter demonstrated that the performance in memory for spatial context decreased in elderly subjects¹. Secondly, contextual colours were shown to be more efficiently processed intentionally. It was observed that instructing subjects to remember the colour of a word improved the recall of this contextual information, but at the expense of item memory, a finding suggesting that intentionality was required to process colours [33,54]. Similarly, Marks [38] showed that recalling pictures (independently of their colour) was worse when the subject's attention had been directed to the colours during encoding, suggesting that processing of colours occupied resources. Finally, Hanna and Remington [24] showed that colours were not bound to specific objects during encoding when attention was not allocated to a deliberate creation of a relationship between specific colours and specific objects. They showed that an incidental encoding did not lead participants to create links between objects and colours, but rather to encode them separately.

Two studies compared precisely the ability to bind central information to its context under incidental or intentional context encoding. Chalfonte et al. [10] and Chalfonte and Johnson [9] proposed a procedure enabling to compare separately, but with equivalent materials, the memory for central information only (drawings of objects), the memory for contextual information only (spatial locations or colours), and the ability to bind central and contextual information together, either intentionally or incidentally. In the *intentional binding* condition, participants were asked to study both central and contextual information. In the *incidental binding* condition, they were instructed to study the central information and no mention was made of the context (thus, context was encoded incidentally). In both conditions, participants were then asked to discriminate previously presented target information, placed in its original context, from distractors in which the central and the contextual information were not correctly paired. They showed that encoding the context intentionally or incidentally did not have the same effect on the recognition of different kinds of contextual information. When the context was spatial information, Chalfonte et al. [10] observed a better performance in normal subjects and amnesic patients following the incidental encoding of the link between objects and locations than when it was intentional. The same result was recently observed with young and elderly adults [37]. On the contrary, when the context was the colour of presentation of the objects, Chalfonte and Johnson [9] observed in young and elderly normal adults that intentional encoding of the link between objects and colours gave rise to a better performance than when it was incidental, though elderly adults were particularly impaired in the intentional condition.

While such behavioural studies investigated the effects of the mode of encoding on the memory for context, little is known about the specific brain correlates associated with both modes of context processing. In fact, several studies have identified the involvement of the prefrontal cortex and hippocampus in encoding and retrieval/verification of information in episodic memory [23,50,51,57,59,60]; (see Nyberg and Cabeza [47] for a recent review). For the most part, these neuroimaging studies focused on cerebral regions involved in item retrieval rather than on the neural substrates of contextual retrieval. However, a few studies have highlighted cerebral regions associated with the retrieval of contextual information, mainly the temporal or spatial context. Spatial context retrieval has been associated with the inferior parietal cortex [32,42,53,56] and left frontal cortex [48], while temporal context retrieval has been associated with the anterior cingulate cortex [48], and parietal and dorsal prefrontal cortices [6,18]. One study associated colour of objects retrieval with the right occipital and temporal cortices [56]. Finally, little is known about structures underlying specific binding processes. Two studies have brought to light the role of the hippocampus in associating information in long term memory [27,28]. In young adults, a recent fMRI study observed activation in the left anterior hippocampus and right prefrontal cortex associated with binding objects and spatial locations in working memory [41].

None of these studies specifically took the conditions of contextual information encoding into account. For example, in the study by Cabeza et al. [6], encoding of the temporal features of the items was incidental. On the contrary, in Nyberg's et al. [48] study, encoding of the temporal and spatial contexts was intentional. Therefore, incidental and intentional encoding were not compared in the same experiment. This question is nevertheless of particular interest since we have already mentioned behavioural studies showing that the retrieval efficiency of different contextual information varies as a

¹ Hasher and Zacks [25] postulated that if an information is processed on an automatic mode, then various factors such as age-differences, intention to encode, or practice, should have no effect on the processing efficiency

function of the mode of encoding, with spatial context best encoded incidentally and colours, intentionally [9,10]. It seems reasonable to postulate that the regions activated during the retrieval of contextual information may differ as a function of the mode of encoding of the context. In fact, the task of retrieving contextual information following its best mode of encoding (e.g. intentional for colours, incidental for spatial locations) might be simpler than following the other mode. A recent observation that the areas involved in information retrieval in episodic memory are different as a function of the difficulty of the retrieval task can help to clarify this problem [46]. Based on a review of the literature, Nolde et al. proposed a model of 'cortical asymmetry for reflective activity' (CARA). In this hypothesis, right and left prefrontal cortices are differentially activated as a function of the relative complexity of retrieval processes. The right prefrontal cortex would be activated in relatively simple episodic memory retrieval situations, e.g. in forced recognition tasks. On the contrary, the left prefrontal cortex would be activated when retrieval imply more controlled processes, such as initiation of self-cueing, or a detailed verification of the retrieved information. Therefore, controlling the mode of encoding of contextual information appears to be crucial.

We designed the present study to explore the brain regions involved in the recognition of items (words) bound to contextual colour features. Our first goal was to examine the specific brain regions involved in binding central and contextual information. Our second objective was to explore the effects of the mode of context encoding (incidental versus intentional) on item-only and item-bound-to-colour retrieval. While items were always encoded intentionally, we compared incidental and intentional encoding of the colour. We chose colour to be the contextual information in the present experiment because, since behavioural studies have demonstrated that an unrelated colour context was best encoded intentionally, we expected to observe differences in areas activated during bound-feature recognition following *incidental* or *intentional binding* conditions.

2. Material and methods

2.1. Participants

Eleven young volunteers (five females, six males) ranging in age from 20 to 32 years (mean age, 23) participated in the study. All the subjects were strictly right handed according to the Oldfield Edinburgh Inventory [52]. The participants were screened to ensure that they were free of any significant previous or current medical disorder. The University of Lie'ge Ethics Committee approved the study, and written informed consent was obtained from all the subjects.

2.2. PET scanning

PET acquisitions were obtained with a Siemens CTI 951 R 16/31 scanner (CTI, Knoxville, TN, USA) in 3D mode. The physical characteristics of the tomograph have been described previously [13]. Subjects had an individual thermoplastic face mask for head stabilisation. A transmission scan was acquired for attenuation correction using three rotating ^{68}Ge sources. Emission scans were reconstructed using a Hanning filter at a cut-off frequency of 0.5 cycles per pixel giving a transaxial resolution of 8.7 mm full width at half maximum and an axial resolution of 5 mm for each of 31 planes, with a total field of view of 10.8 cm in this direction.

For each scan, volunteers received a 30 s intravenous infusion of H_2O^{15} (total activity 6 mCi) through a left forearm canula. A dynamic PET scan consisting of two frames was collected over a period of 2 min (background frame duration 30 s, second frame duration 90 s). The infusion of O^{15} labelled water began 10 s after acquisition start time. Cognitive activation started upon H_2O^{15} infusion, 20 s before the second scan. The integrated counts per pixel recorded during the second scan were used as an index of rCBF [20,39]. All subjects underwent 12 consecutive rCBF measurements, but only eight served for the present analysis (four scans per encoding condition, each condition containing two word-only recognition scans and two bound-feature recognition scans).

2.3. Experimental design

The material consisted of a pool of 240 bi- or tri-syllabic concrete nouns. One hundred and twenty nouns were used for *incidental* colour encoding and the other 120 nouns were used for *intentional* colour encoding. Both lists were equalised for word frequency [4].

The *incidental binding* condition always preceded the *intentional binding* condition. In both incidental and intentional conditions, 60 target words were presented one at a time on a computer screen, every 2 s. Each word was printed in one specific colour, which was not the real colour of the represented object

(for example, the word 'banana' was printed in blue). In order to promote a semantic encoding and to be sure that the subjects processed the words actively, subjects were asked, in both encoding conditions, to make living/nonliving judgements on the words, by pressing a button in the right or left hand, respectively. In the incidental colour encoding condition, subjects were only asked to read the words silently, to make a judgement and to memorise items for a subsequent recognition test. No instructions were given concerning memorisation of the associated colour of the word. In the subsequent intentional colour encoding condition, subjects were asked to memorise both the items and their associated colour and to make living/non-living judgements. Encoding phases were presented outside the scanning period.

The encoding phases in the *incidental binding* and *intentional binding* conditions were each followed by two recognition tests. Participants were first presented with a recognition test for words only, and then with a recognition test for words bound to colours. Each word was preceded by a fixation cross (lasting 500 ms) and appeared on the screen for 2 s, with a white screen appearing during 1.5 s after each word. Firstly, in the word-only recognition test, subjects were shown 30 words (ten targets and 20 distractors). Each word was presented in one specific colour not selected at encoding, in order to avoid the use of colour information as a retrieval cue to retrieve words in memory. Subjects had to recognise the target words, by pressing a left button if the word was a target, or the right one if the word was a distractor. Two scans were performed during the recognition test for words only. Secondly, in the bound words and colours recognition test, subjects were shown 30 words, among which ten target words printed in their correct associated colour, ten target words printed in a colour different from their colour at encoding, and ten distractors. Subjects had to recognise a target word only if the associated colour was correct, by pressing the left button if correct, and the right button when the word was a target item printed in another colour, or when the word was a distractor. Two scans were performed during the recognition test for words bound to colours. Therefore, each subject was scanned eight times: four scans (two during the word-only recognition, two during the bound-feature recognition) following the encoding phase of the incidental binding condition, and four scans (two during the word-only recognition, two during the bound-feature recognition) following the encoding phase of the intentional binding condition (see Fig. 1 for a schematic representation of the PET study and Fig. 2 for the illustration of the paradigm of the recognition memory task).

2.4. PET data analysis

Image analysis was performed on a SPARC workstation (Sun Microsystems, Surrey, UK) using statistical parametric mapping software SPM 96 [22]. Each reconstructed rCBF scan, consisting of 31 primary transverse planes, was interpolated to 52 planes to render the voxels isotropic. The 12 acquisitions from each subject were realigned using the first as reference [66]. The data were then transformed into a standard stereotactic space [61]. A gaussian filter (16-mm full width at half maximum) was applied to smooth each image to accommodate inter-subject differences in gyral and functional anatomy and to suppress high frequency noise in the images. Such transformation of the data allows for pixel by pixel averaging of data across subjects and for direct cross-reference to the anatomical features in the standard stereotactic atlas.

Differences in global activity within and between subjects were removed by analysis of covariance on a pixel by pixel basis with global count as covariate and regional activity across subjects for each task as treatment. [21]. The across-task comparisons were first performed by averaging between paired measurements. For each pixel in stereotactic space, the analysis of covariance (ANCOVA) generated a condition-specific adjusted mean rCBF value (normalised to 50 ml/100 ml/min) and an associated adjusted error variance. The ANCOVA allowed the comparison of the means across conditions on a pixel-by-pixel basis using the *t* statistic. The resulting sets of *t* values constituted statistical parametric maps (SPM(*t*)). The SPM(*t*) were transformed to the unit normal distribution (SPM(*Z*)). Our study was designed to evaluate the effect of the mode of encoding (incidental versus intentional encoding of colour context) on recognition. A conjunction analysis was used to emphasise specific regions associated with the mode of colour encoding. Secondly the effect of binding recognition was compared to item recognition. We used a SPM thresholded at $P < 0.001$, with a further correction for multiple comparisons ($P < 0.05$). SPM was thresholded at $P < 0.001$ (uncorrected for multiple comparisons), when looking for activation in a region predicted from previous studies (voxel or cluster levels).

Fig.1. Schematic representation of the PET study.

BEFORE THE SCAN	DURING THE SCAN			
1 .Incidental colour encoding	Word-only recognition	Word-only Recognition	Bound-feature Recognition	Bound-feature Recognition
2.Intentional colour encoding	Word-only recognition	Word-only Recognition	Bound-feature Recognition	Bound-feature Recognition

Fig. 2. Illustration of the paradigm of the recognition memory task. Subjects studied a list of coloured words before the scan and then performed a recognition test for word-only and for bound features. The encoding of the colour of words was incidental for the first study list and intentional for the second one.

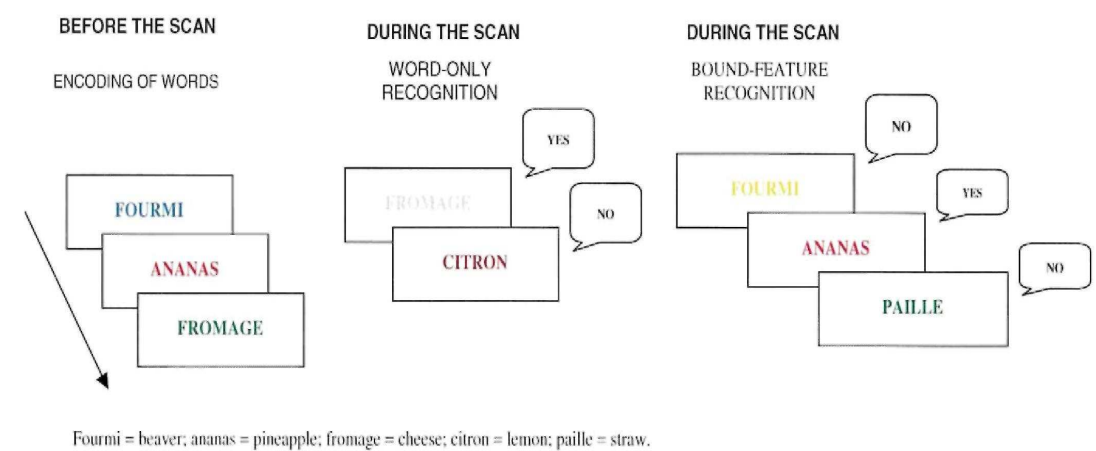
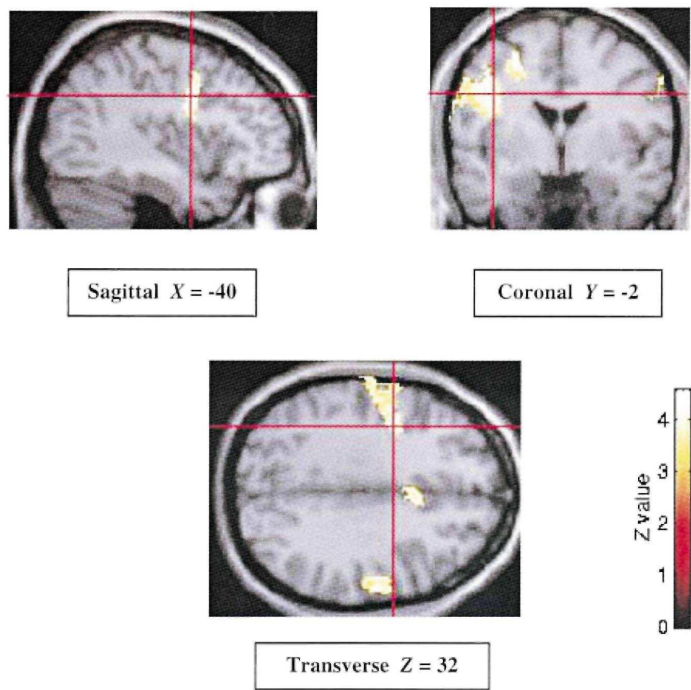


Fig. 5. Recognition of words bound to contextual colours. Different brain regions are engaged along with dorsolateral prefrontal cortex according to the mode (incidental or intentional) of colour encoding.



3. Results

3.1. Behavioural data

A corrected recognition score ($P_{\text{hits}} - P_{\text{false alarms}}$) reflecting accuracy of recognition was computed for each subject. Measures were calculated for each encoding condition (incidental *versus* intentional), respectively for word-only and bound word-to-colour recognition tests.

Means *word-only* and *binding* corrected recognition scores were separately compared between both encoding conditions using the *t*-test (Table 1). Results show a significant difference in *word-only* recognition (*intentional binding* condition < *incidental binding* condition), suggesting that the intentional encoding of contextual colour information disrupted *word-only* recognition. On the contrary, no statistical difference was found in *binding* recognition on the corrected recognition score according to the mode of contextual encoding. At first sight, this result could be considered as contradicting previous findings of an advantage for intentional encoding of contextual colours when compared to incidental encoding.

However, we examined the performance on the recognition of bound words to colours more closely by splitting the corrected recognition score into the number of hits ($W + C +$, target items printed in their correct associated colour), the number of contextual false alarms $W + C -$ (target items printed in another colour) and the number of unrelated false alarms $W -$ (distractor items). Each measure was compared between both encoding conditions (incidental/intentional) using the *t*-test (Table 2). There was no difference in the number of $W + C +$ hits between both encoding conditions. We observed a significant difference between *incidental* and *intentional binding* conditions in the number of contextual false alarms: subjects made less $W + C -$ false alarms in the *intentional* than in the *incidental binding*. We also observed a significant difference between both encoding conditions in the number of $W -$ false alarms: subjects made less unrelated false alarms in the *incidental* than in the *intentional binding* (however, the number of $W -$ false alarms was quite marginal).

3.2. PET results

3.2.1. Effect of the mode of encoding on recognition

The first analysis aimed at contrasting the effects of incidental and intentional modes of colour encoding on brain activation during recognition.

3.2.1.1. Effect on word-only recognition.

We first subtracted word-only recognition following an intentional encoding of the colours from word-only recognition after incidental colour encoding. This analysis showed activation in the left cerebellum (voxel-level) and in the left middle temporal gyrus (BA 21/20, cluster-level) specific to the incidental encoding condition. The temporal activation disappeared when performance was taken as covariable, using either the accuracy score ($P_{\text{hits}} - P_{\text{false alarms}}$) or the false alarm rate.

The inverse contrast (intentional minus incidental) revealed a predominant activation in the left middle frontal gyrus (BA 6) (voxel-level). Other brain regions, more activated after intentional item plus colour encoding (at cluster-level) were the right anterior cingulate gyrus (BA 32), right inferior frontal gyrus (BA 10/47), right postcentral gyrus (BA 3/4), and the left middle frontal gyrus (BA 46). Activation of the two latter regions disappeared when performance was partialled out, using either the accuracy score ($P_{\text{hits}} - P_{\text{false alarms}}$) or the false alarm rate (Fig. 3 and Table 3).

3.2.1.2. Effect on Binding recognition (recognition of both words and associated colours).

The analysis was a subtraction method for binding recognition between both encoding colour conditions. No significant differential cerebral activation was noted at a voxel-level. At a cluster level, PET results during the binding recognition after an incidental colour encoding compared to the intentional one, showed an activation of the left middle temporal gyrus (BA 21/20; -62 -26 -12).

3.2.1.3. Conjunction of each mode of encoding.

We aimed to isolate specific regions involved in recognition as a function of the mode of colour encoding. We carried out a conjunction analysis of the contrasts between incidental and intentional colour encoding in both the *word-only* and *bound-feature* recognition conditions (Fig. 4 and Table 4). A 'masking procedure' was used. The 'mask' consisted of the brain area significantly ($P < 0.05$) activated in both individual subtractions. The conjunction analysis with the masking procedure was designed to examine whether regions specifically involved in recognition after each mode of encoding

had not failed to be highlighted in the contrast analyses. We observed that the cerebral regions significantly activated in the conjunction analysis were included in areas already highlighted in subtraction analyses. The left posterior middle frontal gyrus, along with a few other frontal regions, was confirmed to be activated during the recognition task that followed intentional (effortful) encoding of the second list of words associated with unrelated colours.

3.2.2. Brain activations during bound-feature recognition (contextual link retrieval)

We wanted to highlight the specific regions associated to the contextual (colour) link retrieval according to the mode of colour encoding. Cerebral activations associated with binding recognition minus those of item recognition were contrasted within each encoding modality (Fig. 5 and Table 5).

After incidental colour encoding, bound-feature retrieval was associated with an activation of the left superior parietal lobule (BA 7) and the left middle frontal gyrus (BA 46) (at cluster-level). On the contrary, no significant cerebral activation appeared in the intentional condition. This result is disappointing at first sight. However, a reasonable hypothesis is that the specific activation associated with words bound to colours following an intentional encoding might have been masked by the fact that participants might have already tried to use colours as cues in the word-only recognition. In order to avoid this possible confounding variable and to emphasise the specific brain regions associated to the bound-feature retrieval after an intentional colour encoding, we contrasted cerebral activity for binding recognition after the intentional encoding minus that for word-only recognition after the incidental rather than intentional colour encoding. The results showed a significant cerebral activation in the right superior frontal gyrus (BA 9) (voxel-level). Other brain regions appeared activated (cluster-level): left lingual gyrus (BA 17), left middle frontal gyrus (BA 46) and left precentral gyrus (BA 6). The region of the left middle frontal gyrus (BA 9/46) was significant only when performance was taken as covariable, using either the accuracy score ($P_{\text{hits}} - P_{\text{false alarms}}$) or the false alarm rate.

Table 1 Mean corrected word-only and bound-feature recognition score as a function of the mode of colour encoding

Colour encoding instructions	Corrected score	
	Word-only recognition	Bound-feature recognition
Incidental	0.761 (0.133) ^a	0.247 (0.175)
Intentional	0.634 (0.210) ^a	0.318 (0.231)

^a Significant difference between both word-only recognition scores, $t(10) = -1.241$; $P < 0.05$.

Table 2 Mean proportion of bound-feature recognition for Hits (word+ colour+) and false alarms (word+ colour- and word-) as a function of the mode of colour encoding

Colour encoding instructions	Proportion of			
	Hits W+ C+	Total false alarms	Contextual false alarms W+ C-	Unrelated false alarms W-
Incidental	0.505 (0.196)	0.261 (0.105)	0.245 (0.099) ^a	0.016 (0.017) ^b
Intentional	0.527 (0.203)	0.207 (0.072)	0.161 (0.059) ^a	0.046 (0.037) ^b

^a $t(10) = 2.78$; $P < 0.05$. ^b $t(10) = -3.63$; $P < 0.01$.

Table 3 *Effect of the mode of encoding on word-only recognition*

Brain area	Stereotactic coordinates			Z-score
	x	y	z	
Word-only recognition after incidental minus intentional colour encoding				
<i>P</i> -value <0.001, with further corrections for multiple comparisons				
L cerebellum	-30	-52	-22	4.57
<i>P</i> -value <0.001, tentatively reported (cluster-level)				
<i>L middle temporal gyrus</i> (<i>BA 21/20</i>)	-64	-22	-14	4.14
Word-only recognition after intentional minus incidental colour encoding				
<i>P</i> -value <0.001, with further corrections for multiple comparisons				
L middle frontal gyrus (BA6)	-22	4	48	5.25
<i>P</i> -value <0.001, tentatively reported (cluster-level)				
R anterior cingulate BA (32)	6	10	38	4.47
R inferior frontal gyrus (BA10/47)	44	44	-2	4.41
<i>R poscentral gyrus (BA 3/4)</i>	54	-14	28	4.22
<i>L middle frontal gyrus (BA 46)</i>	-36	40	14	4.11

Regional activations confounded by differences in performances are shown in italic; L, left hemisphere; R, right hemisphere. x, y, z (in mm) refer to coordinates in Talairach space [61].

Fig. 3. *Illustration of significant brain activation direct contrasts between word-only recognition after incidental or after intentional colour encoding. Recruitment of several frontal regions is associated with the later condition*

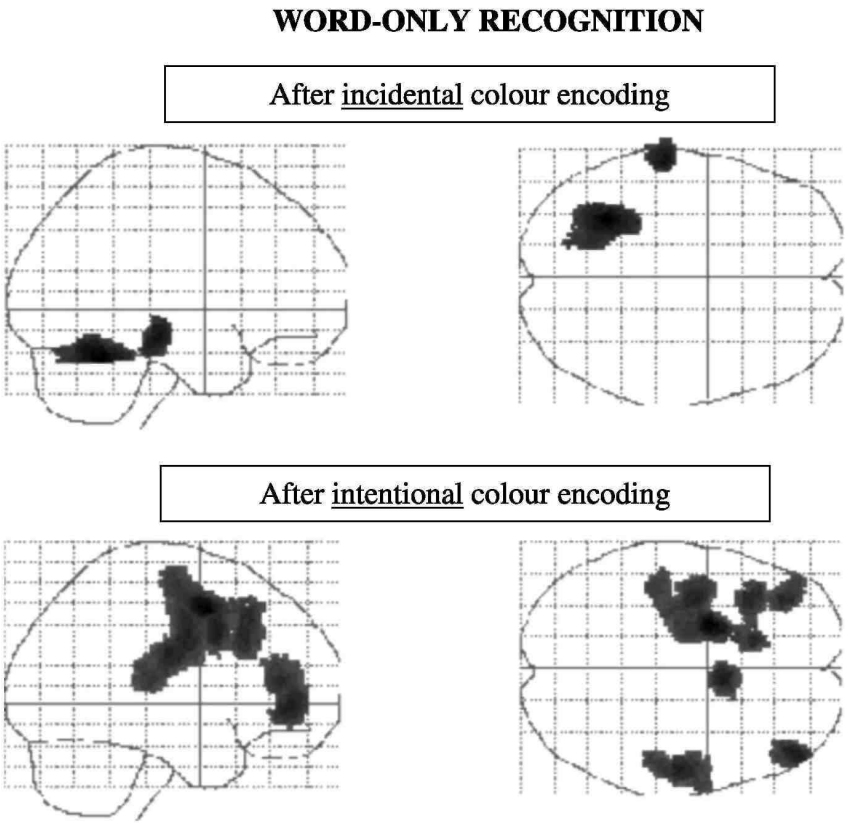
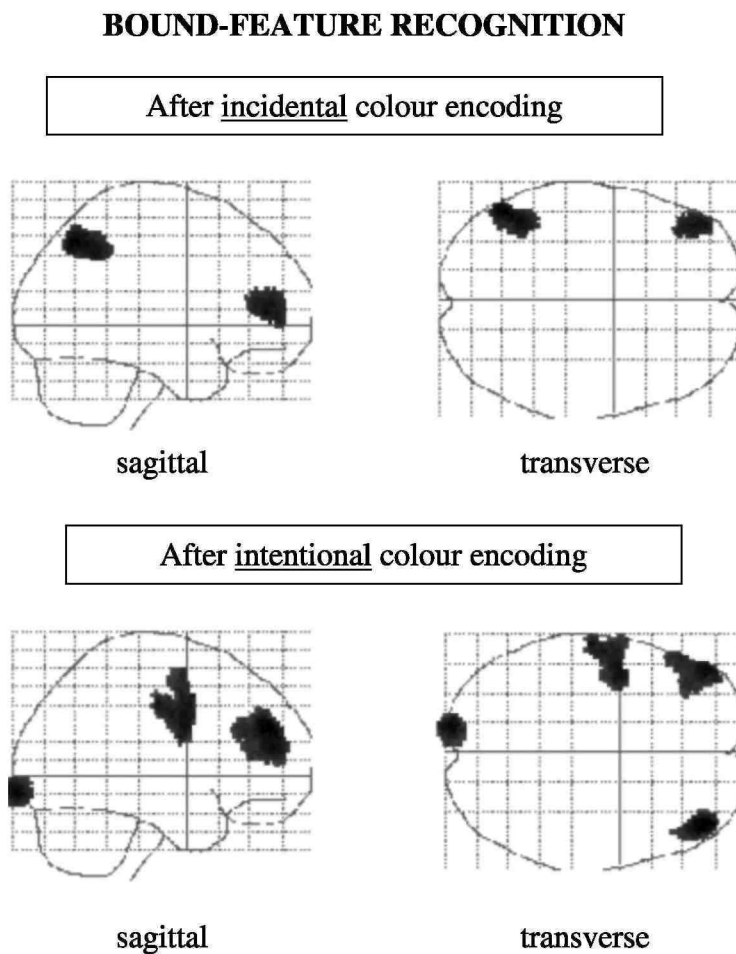


Fig. 4. Significant brain activations of frontal regions for conjunction between word-only recognition and bound-feature recognition following intentional colour encoding.



4. Discussion

The present study was aimed at investigating the cerebral regions involved in recognition of words only and words bound to contextual colours following an incidental or intentional encoding of the context. We are first going to discuss the results collected for the recognition of words only. Then, we will discuss the behavioural and imaging results regarding the recognition of words bound to colours. Finally, we will pay specific attention to the differential effects of the mode of encoding on regions activated during recognition of bound words and colours.

4.1. Word-only recognition

Our behavioural data revealed a better performance in word-only recognition following an *incidental* than an *intentional* colour encoding. This result might reflect both a dual task effect and a specificity of encoding effect. On the one hand, the *intentional binding* condition required participants to process two features (words and colours) together, unlike the *incidental binding* condition in which only words had to be processed. The disruption of word-only recognition in the intentional binding condition might thus only be the result of a dual-task versus simple task discrepancy. On the other hand, both conditions are not equal regarding the specificity of the encoding principle. In our procedure, words in the word-only recognition condition were re-presented in a different colour than the one associated with the word at encoding. In the *incidental binding* condition, participants were not instructed to associate words and colours. Therefore, the change of colours at test might not have disrupted their word recognition. On the contrary, in the *intentional binding* condition, the subject was asked to encode words and their colours together, but in the recognition test, they could not use the colour as a contextual cue to decide whether the word had been previously presented or not. Furthermore, participants had to resist the

interfering effect of new colours associated with the words (e.g. '*I think I saw this word but wasn't it in another colour? Is it the same word?*')

It is worth noting that the performance disruption on word-only recognition in the *intentional binding* condition supports the hypothesis that contextual colours are not processed automatically [25]. This observation confirms those of previous studies, which revealed a better recognition of the link between the central information and the contextual colours when this link had been deliberately rather than incidentally encoded [9, 24, 33–35].

Regarding the cerebral regions associated with the recognition of words only, the subtraction analysis of the cerebral activation for word-only recognition following the two different *binding* conditions revealed greater activation of the left cerebellum and left middle temporal gyrus after *incidental* than after *intentional* colour encoding. The cerebellum and left middle temporal gyrus have been classically described in episodic memory retrieval. Firstly, activation of the left cerebellum has been reported in the retrieval of explicit information (with the contralateral activation of the prefrontal cortex) in a variety of explicit retrieval conditions, e.g. not only during recognition of previously seen words [2,30] or previously heard words [51], for the completion of three-letter stems with previously studied words [3,58], but also during recognition of previously seen faces [26], and for the retrieval of autobiographical information [19].

The precise role of cerebellar activation in explicit memory retrieval remains unclear. Some authors have argued that its activation could complement the process of the retrieval effort of the right prefrontal cortex but this was not the case in our study, since the left cerebellum activation was associated with a *left* prefrontal activation. The cerebellum has also been proposed to contribute to self-initiated retrieval [3] or to be involved in the generation of 'candidate responses' during retrieval [15]. Secondly, the activation of the left middle temporal gyrus is similar to previously reported results for item retrieval [48]. It is probably related to a lexico-semantic process performed on stimuli [65], which is in agreement with the type of processing performed during encoding of words in our study (living/non-living judgements). In a similar manner, the left middle temporal gyrus was activated in a PET study of semantic priming [43] when the cerebral activation in a lexical decision task (to judge if a word or a nonword is a real word) was compared to that in a letter decision task (to judge if the letter *b* is present in consonant letter strings). The activation of the left middle temporal gyrus (BA 21) also frequently appeared in language neuroimaging studies [14] and this region was thus suggested to be part of a semantic processing network. In our study, the activation of the left middle temporal gyrus (BA 21/20) was significant in the conjunction analysis of word-only and bound words and colours recognition following the incidental colour encoding. BA 21 seems to reflect the intervention of lexico-semantic processes in the memory retrieval of words when the encoding is focused on these semantic characteristics.

Word-only recognition in the *intentional binding* condition was associated with the intervention of several frontal regions when compared to word-only recognition in the *incidental binding* condition, e.g. left middle frontal gyrus (BA 6), right anterior cingulate gyrus (BA 32) and right inferior frontal gyrus (BA 10/47). Several parts of BA 6 have already been suggested to be involved in resisting to interference and maintaining temporal order of information [11,12]. Cabeza et al. [6] found increased neural activity of the dorsal prefrontal regions (BA 6) in temporal-order retrieval. In our study, subjects had to learn two lists of words: the first list of words was used for incidental colour encoding and the second list was presented with explicit instructions for intentional colour encoding. It is therefore probable that subjects made more temporal judgements on the words on item recognition following the intentional encoding condition than following the initial incidental one. This hypothesis is supported by the conjunction analysis which revealed significant activation of the left middle frontal gyrus (BA 6) in the item and intentional binding condition, probably reflecting a strategy to resist to interfering colour information and to maintain temporal order of the study lists. Nyberg et al. [48] found the anterior cingulate to be more active during temporal-order than during item retrieval. A similar activation was found in the study of Cabeza et al. [6], but it disappeared when performance was co-varied out. Right anterior cingulate activation was also found in our study, but this activation remained present even after performance was covaried out, suggesting the involvement of this structure in more general processes such as selection of responses [5]. We also tentatively reported greater activation of the right inferior frontal gyrus (BA 10/47) for item recognition in the intentional than in the incidental binding condition (although behavioural performances were worse for word recognition in the intentional binding condition).

This result suggests a role of the right inferior frontal gyrus in the effortful comparison between probe and words held in episodic memory [55].

Table 4: Conjunction analysis of the contrasts between incidental and intentional mode of encoding for word-only and bound-feature recognition

Brain area	Stereotactic coordinates			Z-score
	x	y	z	
Word-only and bound-feature recognition after Incidental colour encoding				
P-value <0.001, with further corrections for multiple comparisons				
L middle temporal gyrus (BA21/20)	-62	-26	-12	5.37
P-value <0.001, tentatively reported (cluster-level)				
R inferior temporal gyrus (BA 20)	54	-42	-22	4.28
Word-only and bound-feature recognition after Intentional colour encoding				
P-value <0.001, with further corrections for multiple comparisons				
L middle frontal gyrus (BA 6)	-24	6	48	5.34
L PrC gyrus (BA 4/6)	-40	-2	32	4.58
<i>L PrC gyrus (BA 6)</i>	-62	-16	42	4.58
<i>R anterior cingulate (BA 32)</i>	6	10	38	4.96
<i>R PrC gyrus (BA 3/4)</i>	58	-12	30	4.61
Regional activations confounded by differences in performances are shown in italic; L, left hemisphere; R, right hemisphere; x, y, z (in mm) refer to coordinates in Talairach space [61].				

Table 5: Cerebral activations during bound-feature recognition tasks minus 'incidental' word-only recognition

Brain area	Stereotactic coordinates			Z-score
	x	y	z	
Bound-feature recognition after <i>incidental</i> colour encoding				
<i>P</i> -value <0.001, tentatively reported (cluster-level)				
<i>L Superior parietal lobule (BA 7)</i>	- 50	-66	48	4.36
<i>L Middle frontal gyrus (BA 46)</i>	- 42	46	8	4.04
Bound-feature recognition after <i>intentional</i> colour encoding				
<i>P</i> -value <0.001, with further corrections for multiple comparisons				
<i>R middle/superior frontal gyrus (BA 9)</i>	40	48	30	4.62
<i>P</i> -value <0.001, tentatively reported (cluster level)				
<i>L lingual gyrus (BA 17)</i>	-14	-94	-10	4.43
<i>L middle frontal gyrus (BA 46)</i>	-46	50	16	4.31
<i>L precentral gyrus (BA 6)</i>	-44	0	30	4.23
<i>L middle frontal gyrus (9/46)</i>	-50	40	30	3.80
Regions associated with different performances are shown in italic. The region in bold appeared only after factoring out performances; L, left hemisphere; R, right hemisphere. x, y, z (in mm) refer to coordinates in Talairach space [61].				

4.2. Recognition of bound items and colours

Behavioural data did not reveal any significant difference between corrected recognition scores for bound words and colours in *incidental binding* and *intentional binding* conditions. However, the number of contextual false recognitions (correct item, incorrect colour) was significantly smaller in the *intentional binding* condition. Though it is only apparent on this last measure, behavioural results support the hypothesis that contextual colours are best processed intentionally. In fact, the crucial role of false recognition in discriminating performances between incidental and intentional context encoding has been observed in various studies [9,10,36,37]. When contextual colours were encoded intentionally, strategies were generated in order to create specifically a link between words and colours. Such strategies could be, for instance, the association of a concept activated by the colour (e.g. sky for the colour blue) with the word into a mental representation or a sentence (e.g. 'the banana is floating in the blue sky').

The use of these encoding strategies could have enabled participants to create an elaborated representation of the word and its context. Therefore, when asked to discriminate between words presented in their correct colour from words presented in a wrong colour, the probability to recognise erroneously a distractor was reduced. On the contrary, when colours were encoded incidentally, attention was focused on the words. Later, when asked to recognise words and their colours, participants might have used their recognition of (or their familiarity with) the words to answer and thus, accepted words even if the colour was not correct. Our results are in line with this hypothesis.

We then aimed at identifying the specific brain regions involved in the retrieval of the contextual information bound with words. The main findings were, on the one hand, the activation of middle prefrontal regions (BA 9/46) in the binding recognition compared to the word-only recognition, and, on the other hand, a parietal activation in the binding recognition compared to the word-only recognition in the *incidental binding* condition.

Firstly, the subtraction of the cerebral activation in word-only recognition from that in *binding* recognition revealed that the activation associated with the *binding* recognition was in the middle prefrontal region (BA 9/46). The activation of the middle prefrontal area (BA 9/46) was also found in episodic memory activation studies and in working memory studies, in which the dorsolateral prefrontal cortex was proposed to be involved in the monitoring of memory responses [55]. Activation of the right midfrontal gyrus was observed in word recognition compared to word identification [30]. For these authors, such an activation was more closely tied to the selection of the appropriate old versus new verbal response or to the contextual memory processing that must be necessary to disambiguate recently studied words from unstudied words in single-word recognition. Henson et al. [29] also described the activation of a dorsal midlateral region in a word recognition task that required reference to the spatiotemporal context of words presented during a previous episode. Compared to activation of a more ventral region of the prefrontal cortex (showing retrieval-related activation that was independent of task instructions), the activation of this dorsal region (BA 46) was associated with increased contextual monitoring requirements.

In our study, activation of BA 9/46 could also reflect the monitoring process in episodic memory because this region appeared activated only in the retrieval of the contextual bound information that required more verification of what was retrieved. As emphasised in behavioural results, BA 9/46 should also be involved in a general strategy used to recognise contextual and unrelated distractors and to monitor responses. For instance, Tulving et al. [63] observed that the medial frontal gyrus (BA 9) was involved in detection of novelty. Unfortunately, neither our design nor the analyses enabled us to specify the brain regions activated when hits or false alarms were produced. Moreover, given the high levels of false alarms during bound-feature recognition, one could suspect that subjects' performance was partly due to guessing. Indeed, our PET design did not permit to include guessing measures or confidence judgements. However, although bilateral frontal activations (BA 9/46) have been previously reported in guessing tasks [16], this interpretation does not fit our results, since the activation of the left frontal region appeared only when accuracy score (hits minus false alarms) or false alarm rates were taken as confounding covariables. Because the influence of the recognition accuracy performance was neutralised in the analyses, one could also reject the hypothesis of a greater frontal activation in bound-feature than in word-only recognition related to increased retrieval difficulties. This confirmed our suggestion concerning a more general role of this left frontal region in a memory search process of the contextual link, independently of retrieval success.

Secondly, a parietal activation was observed when recognition of incidentally bound features was compared to items-alone recognition (under the incidentally encoded colour condition). This

observation suggests the involvement of a fronto-parietal network for selecting candidates to-be-recognised in memory. The parietal activation described in the retrieval of the contextual link in memory is in agreement with some studies also demonstrating such parietal activations in spatial retrieval [32,42,53] and temporal-order retrieval [18]. Our results are in line with the suggestion of Cabeza and Nyberg [7,8] concerning a general role of the parietal regions in context memory. It must be noted, however, that in our study, this parietal activation appeared only in the bound-feature recognition following incidental colour encoding, but not following an intentional one. Our suggestion is that subjects perhaps did not need the activation of the parietal region in the recognition test in the *intentional binding* condition because of the strategies they could have elaborated during encoding and used during retrieval. Thus, in the *intentional binding* condition, reinstating the strategies used during encoding was probably the best way to recognise properly words bound to colours, and this process might have been performed exclusively by prefrontal areas. On the contrary, parietal activation might have been observed as a support to prefrontal activation involved in recognising bound words and colours when the link had been created incidentally. In this case, strategies used at encoding focused on the words and did not include the colours. These strategies were not relevant when it came to recognise the link between words and colours. This suggestion has to be clarified and further studies are needed for a better understanding of the precise role of parietal regions in incidental contextual memory.

Apart from those prefrontal and parietal activations, we expected to observe hippocampal involvement during recognition of bound features. Firstly, according to theoretical accounts [31,40], hippocampal structures should be involved not only in creating and consolidating a link between features associated in a particular event, but also in reactivating this link when the subject is re-presented with the features. In this respect, consolidation and retrieval of bound-feature traces are basically the same process and should equally involve hippocampal structures. Secondly, in a working memory task, Mitchell et al. [41] observed left anterior hippocampal activation in recognition of bound objects and locations. However, our results did not highlight activation of the hippocampus in *binding* recognition compared to *word-only* recognition. This lack of specific hippocampal activation could be explained by the fact that recognising *words only* (words independently of their context) also relies on the retrieval of bound features. Indeed, to decide accurately that a word has already been seen in a preceding phase of the experiment, it is necessary to reactivate the link between this item and the encoding situation (temporal characteristics, mood, semantic associations made at that time, all potentially cueing the recognition). Thus, even if the particular link between word and colour is neglected, there are enough features in the event to require the activation of hippocampal structures (even if the judgement is made on a simple familiarity feeling). Several studies have demonstrated that hippocampal activation already occurs in item retrieval [49,58]. A positive correlation between retrieval success and cerebral activity was shown in the hippocampal region [48], but our study was not designed to create a high level of retrieval success. In both word-only and bound-feature retrieval, there was a low density of target words compared to distractors (10/30 target stimuli).

4.3. Differential effects of the encoding mode

We were interested in regions activated during *binding* recognition following an *incidental* or *intentional* encoding of contextual colours. We observed an activation of the left middle frontal gyrus (BA 46) and left superior parietal lobule (BA 7) in the *incidental binding* condition. On the contrary, the right superior frontal gyrus (BA 9) was activated together with the left middle frontal gyrus (BA 9/46) in the *intentional binding* condition. However, this left frontal activation appeared only when performance were taken as a covariable. These results are consistent with the CARA hypothesis [46], which postulates a prefrontal cortical asymmetry as a function of the complexity of episodic retrieval processes. In fact, previous behavioural studies together with our behavioural data suggest that contextual colour information is best processed intentionally rather than incidentally. Therefore, brain activity should reflect this facilitation of intentional colour encoding on bound-feature recognition. Our results support this hypothesis. Right PFC was activated during recognition following the preferred colour encoding mode. It is reasonable to assume that the discrimination of targets $W + C +$ from distractors $W + C -$ involved only heuristic (rapid) evaluation processes in the *intentional binding* condition. On the contrary, target/dis-tractor discrimination in the *incidental binding* condition probably involved more strategic verification processes, such as generating cues about the encoding situation to retrieve the colour of the word, or comparing the presented word-to-colour combination with the episodic representation of the word in which colour was not included. This makes even more sense when considering that in the *intentional binding* condition, the left prefrontal activation only appeared when performance was a covariable. Thus, a very promising perspective is to investigate a comparable asymmetry for another type of contextual information that is best processed incidentally rather than intentionally, such as spatial locations or temporal order.

5. Conclusion

The present study demonstrated the intervention of different cerebral areas in episodic retrieval according to the mode of contextual encoding. This result supports the hypothesis of a cortical asymmetry for reflective activity (CARA). Moreover, our study isolated the dorsal prefrontal cortex and parietal regions in the retrieval of contextual (colour) bound information, which supports, on the one hand, the monitoring hypothesis and, on the other, the role of the parietal region in contextual retrieval.

Acknowledgements

This work was supported by the Interuniversity Pole of Attraction (IAP) Programme P4/22, Belgian State, Prime Minister's Office, Federal Office for Scientific, Technical and Cultural Affairs, the Belgian National Fund for Scientific Research (FNRS), the Research Fund of Liege University, the Fondation Medical Reine Elisabeth (FMRE), and a grant from the French Community of Belgium (Actions de Recherche Concer-tees-convention 99/04-246). Françoise Lekeu is supported by the IAP. Philippe Marczewski is Aspirant FNRS. Fabienne Collette is researcher at the FNRS. The authors wishes to thank Professor Martin A. Conway and one anonymous reviewer for their helpful comments on an earlier draft.

References

- [1] Andrade J, Meudell P. Is spatial information encoded automatically in memory? *Quarterly Journal of Experimental Psychology* 1993;46A:365-75.
- [2] Andreasen NC, O'Leary DS, Arndt S, Cizadlo T, Hurtig R, Rezai K, Watkins GL, Boles Ponto LL, Hichwa RD. Short-term and long-term verbal memory: a positron emission tomography study. *Proceedings of the National Academy of Science USA* 1995;92:5111-5.
- [3] Backman L, Almkvist O, Andersson JLR, Nordberg A, Winblad B, Reineck R, Langstrom R. Brain activation in young and older adults during implicit and explicit retrieval. *Journal of Cognitive Neuroscience* 1997;9:378-91.
- [4] Baudot J. *Frequences d'utilisation des mots en francais écrit contemporain*. Montreal: Les Presses de L'Université de Montreal, 1992.
- [5] Cabeza R, Kapur S, Craik FIM, McIntosh AR, Houle S, Tulving E. Functional neuroanatomy of recall and recognition: A PET study of episodic memory. *Journal of Cognitive Neuro-science* 1997; 9:277-88.
- [6] Cabeza R, Mangels J, Nyberg L, Habib R, Houle S, McIntosh AR, Tulving E. Brain regions differentially involved in remembering what and when: a PET study. *Neuron* 1997;19:863-70.
- [7] Cabeza R, Nyberg L. Imaging cognition: an empirical review of PET studies with normal subjects. *Journal of Cognitive Neuro-science* 1997;9:1-26.
- [8] Cabeza R, Nyberg L. Imaging cognition II: an empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuro-science* 2000;12:1-47.
- [9] Chalfonte BL, Johnson MK. Feature memory and binding in young and older adults. *Memory and Cognition* 1996;24:403-16.
- [10] Chalfonte BL, Verfaellie M, Johnson MK, Reiss L. Spatial location in amnesia: binding item and location information under incidental and intentional encoding conditions. *Memory* 1996;4:591-614.
- [11] Collette F, Salmon E, Van der Linden M, Degueldre C, Franck G. Functional anatomy of verbal and visuospatial span tasks in Alzheimer's disease. *Human Brain Mapping* 1997;5:110-8.
- [12] Cornette L, Dupont P, Peuskens H, Bormans G, Claeys C, De Schutter E, Mortelmans L, Orban G. Rate dependence of task-related cerebral activations: a PET-study. *Neuroimage* 1999;9:S856.
- [13] Degueldre C, Quaglia L. Performance evaluation of a new whole body position tomograph: the ECAT 951/31 R. In: *Proceedings of the 14th Annual International Conference of the IEEE. EMBS*, 1992:1831-3.
- [14] Demonet JF, Price C, Wise R, Frackowiak RSJ. Differential activation of right and left posterior sylvian regions by semantic and phonological tasks: a positron-emission tomography study in normal human subjects. *Neuroscience Letters* 1994;182:25-8.
- [15] Desmond JE, Gabrieli JDE, Glover GH. Dissociation of frontal and cerebellar activity in a cognitive task: evidence for a distinction between selection and search. *Neuroimage* 1998;7:368-76.
- [16] Elliott R, Rees G, Dolan RJ. Ventromedial prefrontal cortex mediates guessing. *Neuropsychologia* 1999;37:403-11.
- [17] Ellis NR. Is memory for spatial location automatically encoded? *Memory and Cognition* 1990;18:584-92.
- [18] Eyler Zorilla LT, Aguirre GK, Zarahn E, Cannon TD, D'Esposito M. Activation of the prefrontal cortex during judgements of recency: a functional MRI study. *NeuroReport* 1996;7:2803-6.
- [19] Fink GR, Markowitsch HJ, Renkemeier M, Bruckbauer T, Kessler J, Heiss WD. Cerebral representation of one's own past:

neural networks involved in autobiographical memory. *Neuro-science* 1996;16:4275-82.

[20] Fox PT, Mintum MA. Noninvasive functional brain mapping by change distribution analysis of averaged PET images of H_2O^{15} tissue activity. *Journal of Nuclear Medicine* 1989;30:141-9.

[21] Friston KJ, Frith CD, Liddle PF, Dolan RJ, Lammertsma AA, Frackowiak RSJ. The relationship between global and local changes in PET scans. *Journal of Cerebral Blood Flow and Metabolism* 1990;10:458-66.

[22] Friston KJ, Holmes AP, Worsley KJ, Poline JB, Frith CD, Frackowiak RSJ. Statistical parametric maps in functional imaging: a general linear approach. *Human Brain Mapping* 1995;2:165-89.

[23] Grady CL, McIntosh AR, Horwitz B, Maisog JM, Ungerleider LG, Mentis MJ, Pietrini P, Schapiro MB, Haxby JV. Age-related reductions on human recognition memory due to impaired encoding. *Science* 1995;269:218-21.

[24] Hanna A, Remington R. The representation of colour and form in long term memory. *Memory and Cognition* 1996;24:322-30.

[25] Hasher L, Zacks RT. Automatic and effortful processes in memory. *Journal of Experimental Psychology: General* 1979;108:356-88.

[26] Haxby JV, Ungerleider LG, Horwitz B, Maisog JM, Rapoport SI, Grady CL. Face encoding and recognition in the human brain. *Proceedings of the National Academy of Science USA* 1996;93:922-7.

[27] Henke K, Buck A, Weber B, Wieser HG. Human hippocampus establishes associations in memory. *Hippocampus* 1997;7:249-56.

[28] Henke K, Kroll NEA, Behnia H, Amaral DG, Miller MB, Rafal R, Gazzaniga MS. Memory lost and regained following bilateral hippocampal damage. *Journal of Cognitive Neuro-science* 1999;11:682-97.

[29] Henson RNA, Shallice T, Dolan RJ. Right prefrontal cortex and episodic memory retrieval: a functional MRI test of the monitoring hypothesis. *Brain* 1999;122:367-1381.

[30] Jernigan TL, Ostergaard AL, Law I, Svarer C, Gerlach C, Paulson OB. Brain activation during word identification and word recognition. *Neuroimage* 1998;8:93-105.

[31] Johnson MK, Chalfonte BL. Binding complex memories: the role of reactivation and the hippocampus. In: Schacter DL, Tulving E, editors. *Memory Systems*. Cambridge, MA: MIT Press, 1994:31-50.

[32] Kohler S, Moscovitch M, Winocur G, Houle S, McIntosh AR. Networks of domain-specific and general regions involved in episodic memory for spatial location and object identity. *Neuropsychologia* 1998;36:129-42.

[33] Light LL, Berger DE. Memory for modality: within-modality discrimination is not automatic. *Journal of Experimental Psychology* 1974;108:854-60.

[34] Light LL, Berger DE. Are there long-term 'literal copies' of visually presented words? *Journal of Experimental Psychology: Human Learning and Memory* 1976;2:654-62.

[35] Light DD, Berger DE, Bardales M. Trade-off between memory for verbal items and their visual attributes. *Journal of Experimental Psychology: Human Learning and Memory* 1975;104:188-93.

[36] Marczewski P, Van der Linden M, Galluzzo A. Why grandparents should not play spatial memory games with their grandchildren: investigating objects and locations binding in memory throughout the life span. submitted for publication.

[37] Marczewski P, Van der Linden M, Martin C. Binding objects and spatial locations in long-term memory: aging impairs strategic, but not automatic processes. submitted for publication.

[38] Marks W. Effects of encoding the perceptual features of pictures on memory. *Journal of Experimental Psychology: Learning, Memory and Cognition* 1991;17:566-77.

[39] Mazziotta JC, Huang SC, Phelps ME, Carson RE, MacDonald NS, Mahoney K. A noninvasive positron computed tomography technique using oxygen-15 labelled water for the evaluation of neurobehavioural task batteries. *Journal of Cerebral Blood Flow and Metabolism* 1985;5:70-8.

[40] McClelland JL, McNaughton BL, O'Reilly RC. Why there are complementary learning systems in the hippocampus and neocortex: insights from the successes and failures of connection-ist models of learning and memory. *Psychological Review* 1995;102:419-37.

[41] Mitchell KJ, Johnson MKJ, Raye CL, D'Esposito M. fMRI evidence of age-related hippocampal dysfunction in feature binding in working memory. *Cognitive Brain Research* 2000;10:197-206.

[42] Moscovitch MSK, Köhler S, Houle S. Distinct neural correlates of visual long-term memory for spatial location and object identity: a positron emission tomography (PET) study in humans. *Proceedings of the National Academy of Sciences USA* 1995;92:3721-5.

[43] Mummery CJ, Shallice T, Price CJ. Dual-process model in semantic priming: a functional imaging perspective. *Neuroimage* 1999;9:516-25.

[44] Naveh-Benjamin M. Coding of spatial location information: an automatic process? *Journal of Experimental Psychology: Learning, Memory and Cognition* 1987;13:595-605.

[45] Naveh-Benjamin M. Recognition memory of spatial location information: another failure to support automaticity. *Memory and Cognition* 1988;16:437-45.

[46] Nolde SF, Johnson MK, Raye CR. The role of prefrontal cortex during tests of episodic memory. *Trends in Cognitive*

Sciences 1998;2:399-406.

[47] Nyberg L, Cabeza R. Brain imaging of memory. In: Tulving E, Craik FIM, editors. The Oxford Handbook of Memory. New York: Oxford University Press, 2000:501-19.

[48] Nyberg L, McIntosh AR, Cabeza R, Habib R, Houle S, Tulving E. General and specific brain regions involved in encoding and retrieval of events: what, where, and when. *Proceedings of the National Academy of Sciences USA* 1996;93:11280-5.

[49] Nyberg L, McIntosh AR, Houle S, Nilsson LG, Tulving E. Activation of medial temporal structures during episodic memory retrieval. *Nature* 1996;380:715-7.

[50] Nyberg L, Persson J, Habib R, Tulving E, McIntosh AR, Cabeza R, Houle S. Large scale neurocognitive networks underlying episodic memory. *Journal of Cognitive Neuroscience* 2000; 12:163-73.

[51] Nyberg L, Tulving E, Habib R, Nilsson LG, Kapur S, Houle S, Cabeza R, McIntosh AR. Functional brain maps of retrieval mode and recovery of episodic information. *NeuroReport* 1995; 7:249-52.

[52] Oldfield RC. The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia* 1971;9:79.

[53] Owen AM, Milner B, Petrides M, Evans AC. Memory for object features vs. Memory for object location: A positron-emission tomography study of encoding and retrieval processes. *Proceedings of the National Academy of Sciences USA* 1996; 93:9212-7.

[54] Park DC, Mason DA. Is there evidence for automatic processing of spatial and colour attributes present in pictures and words? *Memory and Cognition* 1982; 10:76-81.

[55] Petrides M, Alivistos B, Meyer E, Evans AC. Functional activation of the human frontal cortex during the performance of verbal working memory tasks. *Proceedings of the National Academy of Sciences USA* 1995; 92:5803-7.

[56] Rosler F, Heil M, Henninghausen E. Distinct cortical activation patterns during long-term memory retrieval of verbal, spatial, and colour information. *Journal of Cognitive Neuroscience* 1995;7:51-65.

[57] Rugg MD, Fletcher PC, Frith CD, Frackowiak RSJ, Dolan RJ. Brain regions supporting intentional and incidental memory: a PET study. *NeuroReport* 1997;8:1283-7.

[58] Schacter DL, Alpert NM, Savage CR, Rauch SL, Albert MS. Conscious recollection and the human hippocampal formation: evidence from positron emission tomography. *Proceedings of the National Academy of Sciences USA* 1996;93:321-5.

[59] Squire LR, Ojemann JG, Miezin FM, Petersen SE, Videen TO, Raichle ME. Activation of the hippocampus in normal humans: a functional anatomical study of memory. *Proceedings of the National Academy of Sciences USA* 1992;89:1837-41.

[60] Stern CE, Corkin S, Gonzalez RG, Guimaraes AR, Baker JR, Jennings PJ, Carr CA, Sugiura RM, Vedantham V, Rosen BR. The hippocampal formation participates in novel picture encoding: Evidence from functional magnetic resonance imaging. *Proceedings of the National Academy of Sciences USA* 1996;93:8660-5.

[61] Talairach J, Tournoux P. Co-Planar Stereotaxic Atlas of the Human Brain: 3-Dimensional Proportional System: an Approach to Cerebral Imaging. Stuttgart: Thieme, 1988.

[62] Tulving E. *Elements of Episodic Memory*. Oxford: Oxford University Press, 1983.

[63] Tulving E, Markowitsch HJ, Craik FIM, Habib R, Houle S. Novelty and familiarity activations in PET studies of memory encoding and retrieval. *Cerebral Cortex* 1996;6:71-9.

[64] Vakil E, Tweedy JR. Memory for temporal order and spatial position information: tests of the automatic/effortful distinction. *Neuropsychiatry Neuropsychology and Behavioral Neurology* 1994;7:281-8.

[65] Vandenberghe R, Price CJ, Wise R, Josephs O, Frackowiak RSJ. A common semantic system for words and pictures: functional anatomy. *Nature* 1996;383:254-6.

[66] Woods RP, Cherry SR, Mazziotta JC. Rapid automated algorithm for aligning and reslicing PET images. *Journal of Computer Assisted Tomography* 1992;1:620-33.