The role of prefrontal cortex during tests of episodic memory

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Recent studies of episodic memory using functional neuroimaging techniques indicate that right prefrontal cortex (PFC) is activated while people remember events. Our review suggests that left PFC is also activated during remembering, depending on the reflective demands of the task. As more, or more complex, reflective processes are required (e.g. when criteria for evaluation have to be established and maintained, when the complexity of the evaluation required increases, and when retrieval of additional information is required beyond that activated by an initial cue), left PFC activity is more likely to occur. Our 'cortical asymmetry of reflective activity' (CARA) hypothesis summarizes available findings and suggests directions for future research.

Memory for specific events, such as the occurrence of a word on a particular list (episodic memory), is often contrasted with memory for general information such as the meanings of words (semantic memory)[1]. That is, episodic memories are those for which the mental experience includes information such as time, place, or perceptual detail, that we use to attribute the experience to a particular source[2,3]. Damage to the frontal lobes can impair performance on episodic memory tests[4–6]. In addition, in studies of older adults, lower scores on neuropsychological 'frontal' tasks sometimes are associated with poorer performance on episodic memory tests[7–9]. Consistent with this evidence, studies using positron emission tomography (PET) or functional magnetic resonance imaging (fMRI) to measure the cortical activity associated with episodic memory in healthy young adults have found significant prefrontal cortex (PFC) activity during episodic memory tasks[10–12]. Thus, there is converging evidence of frontal lobe involvement in episodic remembering.

Tulving and colleagues[12–15] (see also Refs 11,16,17) have proposed that left PFC is engaged more than right in encoding processes (specifically, semantic retrieval) and that right PFC is engaged more than left in episodic retrieval processes (i.e. remembering) – the hemispheric encoding/retrieval asymmetry (HERA) model. With respect to episodic retrieval, right frontal activity has been hypothesized to reflect a retrieval 'mode'[18], retrieval effort[19,20], retrieval success[21,22], or post-retrieval evaluation processes[11,23]. Occasionally, increased *left* PFC activity has also been observed during episodic memory tests. However, this activity has not typically been attributed to episodic retrieval, but rather, has often been attributed to semantic retrieval engaged during the episodic test to further encode stimuli that were weakly encoded at study (see Box 1).

Terms emphasizing encoding/retrieval differences suggest that there are processes specific to episodic remembering that are different from the processes involved in encoding. An alternative approach is to assume that the component processes involved in encoding and episodic remembering (and, for that matter, working memory, comprehension, problem-solving, etc.) are drawn from the same set of underlying component subprocesses, although they might be differentially represented in different tasks. Such a component-process approach is described in the multiple-entry, modular memory system (MEM; see, for example, Ref. 24). MEM distinguishes between perceptual processes (e.g. visually locating and identifying external targets) and reflective processes (e.g. processes that, among other functions, sustain, manipulate, revive, and evaluate activation generated by perceptual processes). Reflective processes presumably are subserved by prefrontal cortex in transactions with other brain regions (see Outstanding questions)[25–28]. One possibility is that right PFC subserves a variety of component reflective processes that are sufficient for relatively simple episodic memory tasks, but that more complex episodic memory tasks require additional component processes mediated by left PFC. For example, right PFC might be able, alone, to *refresh* activated information, *shift* between representations, and *note* relations (e.g. whether an item matches a standard), components of many heuristic processes. Left PFC might be recruited for more systematic processes, including *rehearsing*, *initiating* strategies (e.g. recursive operations), and generating cues for *retrieving* inactive information[29,30]. From this point of view, identifying the neural correlates of specific reflective component processes underlying episodic memory might help describe a generic set of component cognitive processes used in both episodic (including encoding and retrieval phases) and

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Box 1. Does left PFC activity during episodic memory tasks reflect additional encoding?

The suggestion that left PFC activity during episodic remembering reflects semantic encoding of test items comes principally from neuroimaging studies contrasting episodic retrieval of stimuli that were strongly encoded with those that were weakly encoded during the acquisition phase. In the studies conducted by Andreasen and colleagues[a–d], strongly encoded stimuli had been rehearsed at acquisition until 100% memory accuracy was achieved whereas weakly encoded stimuli had been presented once just prior to the memory test. These researchers have consistently observed increased left PFC activity for weakly learned test items. Similarly, Buckner *et al.*[e] compared recognition of stimuli after a strong encoding task in which words were categorized as either abstract or concrete ('deep' encoding) with recognition after a weak encoding task in which the letter case in which words were printed was identified ('shallow' encoding). The weak, shallowly encoded items produced increased left PFC activity (BA 44/9) at test relative to the strong, deeply encoded items. Both Andreasen and colleagues and Buckner *et al.* interpret such activity as reflecting additional encoding processes engaged for weakly encoded items, processes less likely to be engaged at test for strongly encoded items because they were more completely processed during acquisition.

One problem with this idea is that it fails to account for why participants would intentionally engage in additional encoding of poorly learned items at test (e.g. how does this activity facilitate recognition?). If, alternatively, this additional encoding is thought to be relatively 'automatic' in nature, engaged whenever items that have not been strongly encoded are presented, this raises the question of why this automatic encoding was not engaged during the acquisition phase to begin with. More important, regardless of how one construes the nature of the additional encoding processes, the notion that test items that were poorly encoded at study result in additional encoding at test is not supported by the outcomes of neuroimaging studies comparing recognition of old and new items. The 'additional encoding' account of left PFC activity during episodic remembering should predict that new items at test, having received little or no recent encoding, should produce significantly more left PFC activity than the old items at test. However, of the five studies in Table 1B that directly compared recognition for blocks of old (or mostly old) to blocks of new (or mostly new) items[f–j], old items produced significantly more left PFC activity than did new items in all but one of these studies[h].

References

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'non-episodic' tasks. Similarly, insights about PFC function with respect to episodic memory are likely to emerge from studies of other tasks (e.g. working memory[31,32]) that draw on the same set of component reflective processes.

Several lines of evidence suggest that left PFC might play a central role in more complex episodic remembering, especially under conditions demanding more systematic component processes. Unilateral left PFC damage can produce marked deficits in word-stem cued-recall[33] and in autobiographical recall[5]. Furthermore, left PFC damage can produce a deficit in source memory (e.g. who it was that said something) in the absence of a significant deficit in identifying which items were previously experienced (old/new recognition[5]). Compared with old/new recognition, source identification decisions require more episodic information (e.g. time, place, modality, speaker, etc.) and tend to be more reflectively demanding, as evidenced by, for example, their (often) longer time course[34] and greater disruption from distracting secondary tasks[35].

To investigate neural activity correlated with the episodic demands of a task, Johnson *et al.*[23] contrasted the cortical activity (as measured by event-related potentials, or ERPs) for old/new recognition and source identification (in this case whether an item was presented as a picture or a word). They found a right-lateralized positivity at frontal sites, present during both old/new recognition and source identification tasks, that they suggested was in accord with the right PFC activity observed with PET and fMRI in episodic memory tasks generally. Equally important, they also noted a second frontal component associated with the difference between old/new recognition and source identification. This difference was evident bilaterally, but subsequent examination of data from electrodes placed more laterally than those reported in Johnson *et al.*, suggested that this second component tended to be left-lateralized (S.F. Nolde and M.K. Johnson, unpublished data). Converging evidence was obtained from an fMRI study: greater left PFC activity was seen when participants identified whether items had been presented previously as pictures, words, or were new items, than when they simply identified whether an item was old or new[36]. Other recent neuroimaging studies of source identification (temporal discrimination[37] and location identification[38]) have also found left PFC activation.

To further explore the possibility that variations in the reflective demands of different episodic tasks is associated with differential left PFC activity, we reviewed the neuroimaging literature, including those studies considered in earlier reviews as well as more recent experiments. We examined studies of recognition, cued-recall, and free-recall where frontal activations were reported, classifying each experiment in terms of the level of presumed reflective demands[39]. For example, we contrasted the PFC regions of activation found in less reflectively demanding recognition tasks with the PFC regions of activation found in more reflectively demanding recognition tasks. We expected that, on average, tasks in which participants were engaged in more complex, reflective processes would be more likely to have resulted in left PFC activity than would memory tasks which were less complex.

PFC activations associated with old/new recognition

Table 1(A–C) shows Brodmann's areas for the left and right PFC activations observed in 19 PET and fMRI studies of old/new recognition memory (i.e. categorizing test items as either old or new). To operationalize the level of reflective processing required by the tasks, the studies were assigned to Table 1A and 1B using the single criterion of whether the tasks involved forced-choice recognition (Table 1A) or sequential old/new (sometimes called yes/no) recognition (Table 1B). In the six studies included in Table 1A, participants performed a relatively simple forced-choice recognition task requiring them to indicate which of two simultaneously presented stimuli (one old and one new) had been previously presented during the acquisition phase. In the 12 studies included in Table 1B, participants were presented with one test stimulus at a time and indicated whether or not they remembered seeing it during the acquisition phase (i.e. they identified each stimulus as being either 'old' or 'new').

Forced-choice tests are generally thought to be easier than sequential (yes/no) recognition tests[40,41]. Small differences between old and new distributions in familiarity (or any feature) will not be as discriminable in sequential recognition as in forced-choice tasks; hence, participants in the sequential recognition tasks should be more likely to attempt to retrieve and evaluate additional episodic detail. In addition, in the sequential, but not the forced-choice test, participants must develop and maintain an appropriate criterion for evaluating memory characteristics (based upon the distributions of old and new items) evoked by test items. In doing so, participants might retrieve prior items and decisions in order to adjust their criteria for subsequent test trials. Thus, the reflective demands of the sequential recognition tests in Table 1B are greater than those of the forced-choice recognition tests in Table 1A.

Cortical activity associated with the presumably less demanding forced-choice recognition (Table 1A) was restricted to the right PFC. In contrast, the cortical activity associated with more reflectively demanding old/new recognition tasks (Table 1B) was significant in both the left and right PFC for the majority of the studies. Thus, while the right PFC seems to be activated independent of the specific test conditions, the left PFC (either independently, or in conjunction with the right PFC) is activated under more reflectively demanding test conditions.

One possible confounding factor is that nonverbal materials were used for studies in Table 1A, whereas verbal materials were used for most studies in Table 1B. Given the well-established association between the left hemisphere and linguistic function, the left PFC activity in Table 1B might well be attributed to the verbal nature of the stimuli[56]. However, the Andreasen *et al.*[52], Schacter *et al.*[51] and Tulving *et al.*[53] studies in Table 1B used nonverbal stimuli and all observed left PFC activity. Also, the Moscovitch *et al.*[44] and Owen *et al.*[46,47] studies in Table 1A used pictures of verbalizable, common objects[57]. This suggests that the differences in the left PFC activity observed in Table 1 do not simply reflect differences in the materials used.

Table 1. Left and right PFC activations associated with recognition

	Brodmann areas	
	Left PFC	**Right PFC**
A Simple old/new recognition		
Haxby *et al.*[42]	–	10/46/45
Grady *et al.*[43]		
older adults	–	10/46, 47
Moscovitch *et al.*[44]		
spatial	–	44, 45, 46
object	–	44, 46
Haxby *et al.*[45]	–	10, 9/45, 8/44
Owen *et al.*[46]		
object-location	–	9, 11, 47/11
location	–	9, 45/47, 44
Owen *et al.*[47]		
object features	–	47/12
B Complex old/new recognition		
Jones-Gotman *et al.*[48]	–	yes
Tulving *et al.*[49]	–	10, 46, 44(9)
Andreasen *et al.*[50]		
long-term	10	10, 46, 47, 9
short-term	10	10/47/9
Kapur *et al.*[19]		
low target	10	10, 46, 9
high target	10	10, 46, 9
Nyberg *et al.*[18] [(a)]		
old items > new items	10/47	11
Schacter *et al.*[51]		
possible objects	10, 44/47	–
Andreasen *et al.*[52]	yes	yes
Rugg *et al.*[21]	10	10, 46
Tulving *et al.*[53]	10/9/46, 8/44, 46/45/10/9	10, 9, 46
Busatto *et al.*[54]	46	–
Cabeza *et al.*[13]	–	10, 45, 47
Rugg *et al.*[55]		
shallow encoding	–	10, 46/9
deep encoding	44,9	46/9
C Direct comparisons of complex to simple recognition		
Buckner *et al.*[22]	44/9, 44/45	44/45

[a] *Results from comparisons of three different stimulus conditions each to the control task were omitted because only activations commonly observed across the three comparisons were reported. Thus, the full extent of activation was not available.*

Table 2. Left and right PFC activations associated with cued and free-recall

	Brodmann areas	
	Left PFC	**Right PFC**
A Simple cued-recall		
Shallice *et al.*[11]	–	10/46, 47
Fletcher *et al.*[58]	–	10/46
Petrides *et al.*[56]	–	9/46, 11
Buckner *et al.*[59]		
compared to repetition	–	yes
compared to rest	yes	–
Cabeza *et al.*[13]	–	47
B Complex cued and free-recall		
Buckner *et al.*[60] (a)	8/9 (b)	10, 8/9, 8, 9
Petrides *et al.*[56]	9/46, 45	9/46, 9
Blaxton *et al.*[62]		
word pairs	10	10, 9, 46, 47
word fragment	10, 11	10, 46
Bäckman *et al.*[61]		
younger adults	10/46 (c)	10/46
older adults	10/46	10/46
C Direct comparisons of complex to simple cued-recall and free-recall		
Grasby *et al.*[63]	10/46	10/46
Andreasen *et al.*[64]		
complex narratives	yes	–
Andreasen *et al.*[65]		
word lists	yes	yes
Fletcher *et al.*[66]	yes	yes
Schacter *et al.*[20]		
young adults	10/46	–
Schacter *et al.*[67]		
older adults	10, 44	11

[a] *Reported here is the overall analysis of experiments 1–3, which include data reported earlier in Squire et al.*[10]
[b] *Not significant when six-fold Bonferroni correction applied.*
[c] *Nearly significant,* $t_{observed}=4.48$ *with* $t_{critical}=4.52$

A second possible confounding factor is related to the specific contrast performed in the analysis of the neuroimaging data. All of the studies included in Table 1A compared the cortical activity observed during the recognition task to the activity observed during a separate control task (e.g. a stimulus matching task[45]). In contrast, five of the studies included in Table 1B compared the cortical activity during recognition for blocks of old items (i.e. all or nearly all of the test stimuli were old) to the cortical activity during recognition for blocks of new items[18,21,49,51,53]. However, the remaining seven studies included in Table 1B used a contrast similar to that used in the studies included in Table 1A and five of these showed left PFC activity. Thus, observed differences between Tables 1A and B in left PFC activity are unlikely to reflect differences in the contrast tasks.

A direct comparison of difficulty is provided by Buckner *et al.*[22] who observed the cortical activity associated with recognition for word stimuli under conditions which effectively varied the difficulty of the test (Table 1C). During the initial acquisition phase, participants performed two different encoding tasks designed to vary the success of recognition at test. For one set of items, participants performed a shallow encoding task, identifying the case (i.e. upper or lower) in which the acquisition words were presented. For a separate set of items, they performed a deep encoding task, identifying each item as either abstract or concrete. As expected, during the recognition test more items were correctly identified as old in blocks of items encoded with the deep task (85%) than blocks encoded with the shallow encoding task (47%). The manipulation of recognition performance between the deep and shallow encoding conditions can also be thought of as a manipulation of the complexity, or difficulty, of the recognition task at test. Consistent with the notion that differences in results of studies in Tables 1A and B are related to the complexity of the test task, rather than the verbal or nonverbal nature of the stimuli, Buckner *et al.* observed greater activation in the left (as well as right) PFC with the items encoded in the shallow task (i.e. difficult recognition) compared with items encoded with the deep task (i.e. easy recognition). (However, for an inconsistent finding see Rugg *et al.*[55]) It should be noted that although weakly encoded old items might require more complex processing at test than strongly encoded old items, it does not follow that recognition during blocks of all *new* test items will produce the most complex processing. Rather, blocks of new items might result in simple heuristic evaluation based largely on undifferentiated familiarity information, processing primarily supported by right PFC.

PFC activations associated with cued and free-recall

Table 2(A–C) shows the left and right PFC activations observed in 15 PET and fMRI studies of cued-recall (i.e. at test, participants were presented stimuli which served as a cue to help them remember specific items learned during acquisition) and free (uncued) recall. Studies were assigned to Tables 2A and 2B using two criteria: first, whether only old cues (cues presented at study with to-be-remembered items) or old and new (not studied) cues were presented during the test phase, and second, whether or not there was a strong association between the cue and the to-be-remembered item. In the studies in Table 2A, only old cues were presented during the test phase and the association between the test cue and the to-be-remembered items, composed of word pairs learned during the acquisition phase, was relatively strong. Shallice *et al.*[11] and Fletcher *et al.*[58] used category-exemplar combinations (e.g. poet–Browning), with the category label serving as recall cue at test, and Buckner *et al.*[59] used related noun–verb combinations (e.g. wheel–spin), with the verb serving as the recall cue at test. Although in the Petrides *et al.*[56] study the word-pairs were unrelated (e.g. truck–eagle), participants were required to learn only five pairs that were rehearsed during the learning phase until 100% accuracy was achieved. Similarly, in Cabeza *et al.*[13], the duration and repetition of the unrelated word-pairs during the learning phase, and the amount of delay between the acquisition and test phase, were designed to maximize cued-recall performance.

In contrast, the cued-recall studies included in Table 2B all presented participants with some old and some new cues randomly intermixed at test. Equally important, in these studies, the association between the test-cues and the to-be-remembered items was relatively weak. Buckner *et al.*[60] and Bäckman *et al.*[61] used a word-stem cued-recall task in which three letter word-stems (e.g. GAR) were presented at test and participants recalled the acquisition word with which the word-stem could be completed (e.g. GARNISH). Each of the three letter word-stems could be completed with non-studied words (e.g. GARAGE) as well as the target, and the stems had not been presented along with the words at study and did not provide any semantic cue for the response. Blaxton *et al.*[62] presented test stimuli constructed by omitting every other letter from each word (e.g. for the study word EAGLE, participants were tested with E_G_E). In addition, Blaxton *et al.* also examined cued-recall with weakly associated word-pairs learned under conditions in which, unlike Cabeza *et al.*[13], no effort was made to enhance recall performance with the acquisition task. Also included in Table 2B is a study of free-recall by Petrides *et al.*[56] in which participants attempted to remember as many items from a 20-word list as possible during the test phase. Participants could recall the words in any order that they wished, but were instructed to continue recalling the acquisition list throughout the 60-second scanning period, starting the task over when they could no longer remember any new words.

In short, the cued-recall tests in Table 2B were more reflectively demanding than the cued-recall tests in Table 2A. In contrast to the studies in Table 2A, using weakly associated old cues or new cues at test should be less likely to immediately activate an old item thus requiring additional self-cueing and comparison and selection among candidate responses. For new cues in the Table 2B studies, participants would be more likely to generate several possible solutions, judging whether each had been included during the acquisition phase. Likewise, because old word-stems in Table 2B could be completed with words other than those that had been previously presented (and the stems are not highly associated with the target item) participants are likely to have generated more than one solution before attributing one to the acquisition list (also a possibility with the old word-pairs in Blaxton *et al.*[62]). Thus, in order to perform the cued-recall task with intermixed old and new cues, participants would have had to engage additional, reflective operations for generating, maintaining, and evaluating the episodic status of possible solutions. Similarly, compared with the cued-recall studies in Table 2A, the Petrides *et al.*[56] recall task is also more likely to involve additional reflective functions, including those processes related to self-initiated cueing and retrieval, and selection among candidate responses, as well as processes required for recycling through the list in the case of free-recall.

Consistent with the notion that the cued-recall tasks in Table 2B were more reflectively demanding, the percentage of correctly recalled items was significantly higher for the studies in Table 2A (84%) than for those in Table 2B (65%) [$t(8)=3.00$; $P<0.05$], excluding the results for older adults in Bäckman *et al.*[61] who recalled only about 27% of the to-be-remembered items. Most important, with the single exception of Buckner *et al.*[59], the PFC activations in studies in Table 2A were restricted to the right hemisphere and in Table 2B were present in both the left and right hemispheres. Interestingly, in the Buckner *et al.* study participants were also instructed to recall the perceptual detail (source) that was encoded with to-be-remembered items during acquisition (e.g. remember the image for items presented as pictures); the additional reflective activity required by source identification might account for the left PFC activation.

Studies directly comparing simple and complex cued-recall are presented in Table 2C. Fletcher *et al.*[66] compared cued-recall under conditions where the words within a pair were either highly related (e.g. king–queen) or not related (e.g. puppy–hurricane). As one would expect, cued-recall performance was better for the related word pairs (81% compared with 76%), although this difference was not significant. Compared with the related word-pairs, unrelated word-pairs produced significantly greater activation in both left and right PFC. Similarly, Schacter *et al.* manipulated the difficulty of a word-stem cued-recall task for young[20] and older adults[67] by varying the type of encoding during the acquisition phase. In one encoding task, designed to yield high recall success, acquisition items were presented four different times during which participants engaged in a semantic judgment for each word (i.e. counting the number of meanings associated with the word). In a second encoding task, designed to yield low recall success, acquisition items were presented only once during which participants engaged in a nonsemantic judgment for each word (i.e. counting the number of T-junctions present in the word). During the test phase, participants performed the word-stem cued-recall task for blocks of high and blocks of low success items. As intended, participants' cued-recall performance was better in the high (79% and 65% correctly recalled for young and older adults respectively) than in the low (35% and 26%) condition. As discussed earlier, given a shallow encoding task, a test cue should be less likely to directly activate a studied item thus requiring additional complex reflective processing at test including self cueing, evaluating more candidate responses, etc. The Schacter *et al.* results corroborate the general pattern of results already discussed, with greater activity in left PFC (although interestingly not in right PFC for young adults[20]) for the more demanding cued-recall task.

Table 2C also includes three studies directly comparing simple and complex free-recall. Andreasen *et al.*[64,65] manipulated the acquisition conditions in which participants initially encoded stimuli. For both complex narratives[64] and word lists[65], participants recalled to-be-remembered items that had either been highly practiced (i.e. to-be-remembered items were repeatedly presented until 100% accuracy was achieved, and were easy to recall at test) or were unpracticed (i.e. to-be-remembered items were only presented once, and were difficult to recall at test). As expected, free-recall performance was indeed better for items that had been highly practiced (97% and 95% for complex narratives and word lists respectively) than for items that were unpracticed (56% and 44%). Most critical, more left PFC

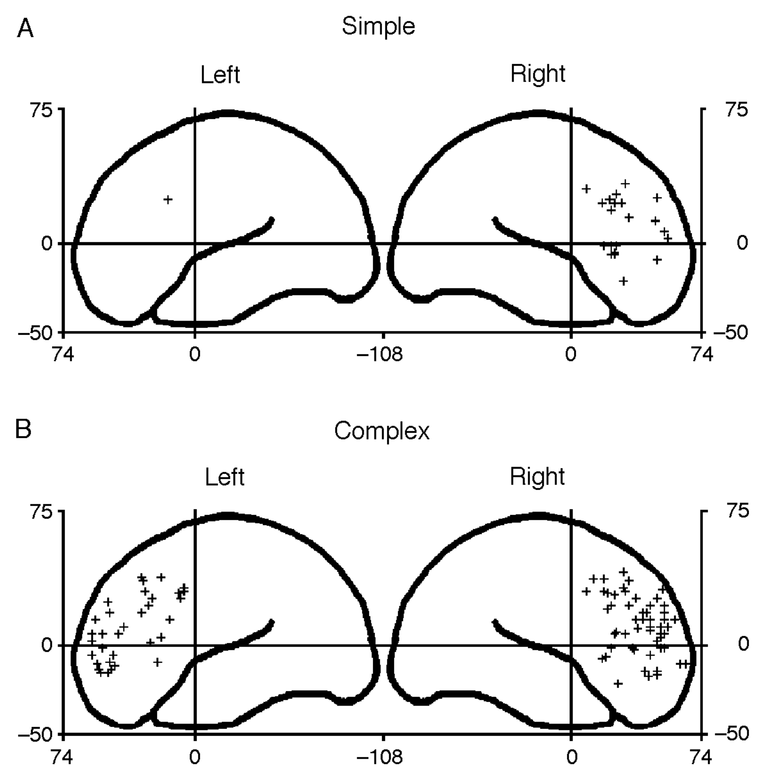

Fig. 1 Talairach coordinates (when provided) for activations during simple (A) and complex (B) episodic remembering for studies reported in Tables 1 and 2. Note that for some studies more than one activation was reported for a given Brodmann area (BA), so that the number of individual activations identified in this figure exceeds the number of discrete BA areas reported in Tables 1 and 2.

activity was observed for the free-recall of unpracticed test items (complex free-recall) when compared with the highly practiced test items (simple free-recall). Grasby *et al.*[63] examined the effect of increasing word-list length on the cortical activity associated with free-recall. As with the manipulation of encoding tasks described above, the effect of increasing the number of to-be-remembered words should make the subsequent free-recall a more complex task to perform, requiring, for example, more self-initiated retrieval and keeping track of which items had already been recalled. Consistent with this notion, the percentage of items correctly recalled at test declined as the number of the to-be-remembered items increased, dropping from 100% accuracy with only two items down to 62% accuracy with 13 items. Furthermore, regions of prefrontal cortical activity that were positively correlated with the increase in list-length were present in both the left and right PFC.

Outstanding questions

- To what extent do episodic memory and other higher-order cognitive tasks, such as working memory, comprehension, problem solving, and decision making, involve the same or different component processes, or the same or different neural substrates?
- Are more complex reflective processes a function of left PFC or a cooperation between left and right PFC, or some mixture of these two possibilities? Are the component processes of simple, heuristic and more complex systematic processes different, or are they similar processes that are used either heuristically or systematically?
- How is PFC organized with respect to different reflective processes (e.g. *refreshing*, *shifting*, *noting, rehearsing, retrieving*) and representations (e.g. auditory, visual, spatial, linguistic)? There are at least five possible models. Model 1: distinct PFC regions are associated with different reflective processes independent of the nature of the representations the processes operate on. Model 2: distinct PFC regions are associated with different types of representations engaged, independent of the type of reflective process performed on those representations. Model 3: there are different PFC regions for specific combinations of reflective process and type of representation (e.g. refresh color, refresh location, refresh object, etc.; note color, note location, note object, etc.). Model 4: PFC regions are dedicated neither to reflective processes, nor to types of representations, nor to unique combinations of process and representation; rather, a PFC region's function changes flexibly depending on its transactions with other regions. Model 5: a hybrid model in which characteristics of Models 1–4 are exhibited throughout PFC (i.e. different regions of PFC correspond to different models).

Conclusions

Clearly, right PFC is activated during episodic remembering as Tulving and others have observed[12]. However, left PFC is activated under certain conditions as well. Figure 1 plots the Talairach coordinates (when reported) for the studies in Tables 1 and 2, and shows a striking pattern of results – left PFC activations are likely when the reflective demands of the memory task are relatively complex. This pattern suggests a 'cortical asymmetry of reflective activity' (CARA) hypothesis. According to this idea, heuristic processes are primarily enabled by right PFC. Such heuristic reflective processes (e.g. temporary maintenance of activated information and comparison to a 'standard' or criterion, or in the case of forced-choice recognition, the comparison of two stimuli on some dimension) are sufficient for episodic memory tests that are relatively simple. In contrast, more systematic processes – processes that are engaged when episodic memory tests demand, for example, more detailed, deliberative analysis of activated information, maintenance of information while it is being evaluated, or the initiation of systematic self-cueing to retrieve additional information[29] – are primarily supported by or require left PFC. (It should be noted that tasks that differ in difficulty, as measured, for example, by response time, do not necessarily differ in processing complexity; some more difficult tasks might engage additional heuristic processing, and would produce increased right PFC activity relative to less difficult heuristic tasks).

The CARA hypothesis also suggests that the association of right PFC with retrieval and left PFC with encoding[12] might reflect a difference in the processing requirements of the retrieval and encoding tasks that have been compared. That is, the observed empirical regularity described by the HERA hypothesis might arise because encoding tasks frequently used require on average more reflectively complex processing than do the retrieval tasks frequently used. A related point is that although we have discussed the activations in left and right PFC in the context of the episodic memory tasks in which they were observed, we are by no means suggesting that these cortical regions, and processes which they support, are uniquely associated with episodic memory tasks. More likely, the PFC activations observed during the remembering of episodic events are associated with reflective processes that are common to a variety of different tasks. For example, left PFC activation increases as problem solving tasks become more complex[68] or semantic tasks require more selection of information from among competing alternatives[69]. Thus, the specific processes with which the left and right PFC are associated might be best thought of in the context of more general component process architectures[39,70,71] rather than as processes dedicated to any one particular task, such as episodic retrieval.

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Implicit learning: news from the front

Axel Cleeremans, Arnaud Destrebecqz and Maud Boyer

Can we learn without awareness? While the current consensus is most likely to be 'no', there is, however, considerable ongoing debate about the role that consciousness plays in cognition and about the nature of consciousness itself. In this article, we review recent advances in the field of implicit learning, based on three perspectives: empirical findings (including neuropsychological evidence), methodological issues, and theoretical positions (including computational models). The overall picture that emerges is complex and reflects a field that is very much in flux: while it seems undeniable that cognition involves some form of unconscious processing, it is as yet unclear how to best separate conscious and unconscious influences on learning, and how to best think about the status of the 'cognitive unconscious'. We suggest that implicit learning is best construed as a complex form of priming taking place in continuously learning neural systems, and that the distributional knowledge so acquired can be causally efficacious in the absence of awareness that this knowledge was acquired or that it is currently influencing processing, that is, in the absence of metaknowledge.

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Implicit learning (IL) – broadly construed, the ability to learn without awareness – has been under investigation for over thirty years, but it is only recently, through a renewal of interest both in learning and in consciousness, that the phenomenon has attracted widespread attention[1–8]. According to one of the most common and conceptually neutral definitions of IL[9], learning is implicit when we acquire new information without intending to do so, and in such a way that the resulting knowledge is difficult to express. In this, implicit learning thus contrasts strongly with explicit learning (e.g. as when learning how to solve a problem or learning a concept), which is typically hypothesis-driven and hence

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