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The relationships between episodic memory, working memory, and executive functions: the contribution of the prefrontal cortex

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Abstract

The purpose of this article is to review recent data regarding the relationships between the prefrontal cortex and memory processes. Numerous questions are addressed: are the memory impairments following a frontal lesion qualitatively different from those following other kinds of lesions? Do the memory deficits following a frontal lesion impair specifically memory functioning or are they secondary to more general disorders affecting the strategic organisation of the cognitive processes? Is the link between some memory impairments and the frontal areas exclusive or not? The article also reviews the neuroimaging studies aimed to identify which frontal regions underlie the working memory and episodic memory processes and the relations between them. Taken as a whole, these studies demonstrated that similar cerebral areas are involved in tasks requiring working memory and episodic memory processes as well as executive functions. These data could indicate that these quite different tasks require the intervention of similar cognitive mechanisms

Numerous neuropsychological studies have demonstrated that frontal association cortex lesions disrupt various aspects of encoding and retrieval in episodic memory (see Mayes & Daum, 1997; Van der Linden, 2000; Wheeler, Stuss, & Tulving, 1995). More specifically, damage to this brain region has been reported to impair free recall more than recognition, to affect temporal order and source memory as well as some kinds of metamemory processes, and also to increase susceptibility to interference. It has been suggested that the prefrontal lesions disrupt the executive processes that are important in effortful and plan-dependent encoding and retrieval processes, especially the organizational processes necessary for optimal memory encoding, formulation of detailed retrieval strategies, and verification of candidate memories.

Indeed, encoding often requires a person to relate the different components of an episode together as well as to information already existing in long-term memory (see Lockhart & Craik, 1990). In other words, memory performance may be maximized by spontaneously undertaking various cognitive operations including strategies of organization or categorization of the material to be remembered, mental imagery, using verbal mediators, etc. In addition, a distinction is generally made between associative and strategic retrieval processes (see Schacter, Norman, & Koutsaal, 1998; Moscovitch, 1989). Associative processes enable the automatic activation of a memory trace if there is a sufficient matching between the information contained in the retrieval cue and that contained in the trace. This interaction between a cue and a stored trace makes the retrieved information available in the form of a conscious memory (the ecphoric process; Tulving, 1983). Strategic retrieval processes set up an active research that allows reinstating a retrieval context from which retrieval cues will operate. In other terms, when the retrieval cues provided to a person in order to retrieve an episode do not include enough specific information for ensuring a successful setting up of the associative processes, they must be submitted to elaborative processes until they match the memory trace in a sufficient way. It should be noted that other aspects of retrieval processing have been distinguished (see Rugg & Wilding, 2000): retrieval mode is considered to be a tonically maintained cognitive state (or 'set') entered when there is a need to engage in episodic retrieval; retrieval orientation refers to the specific form of the processing that is applied to a retrieval cue (for example, orientation would differ according to whether the memory task requires retrieval of phonological or spatial information); retrieval effort refers to the level of processing resources devoted to a retrieval attempt; and retrieval success denotes any process associated with ecphory.

When a successful matching is reached, it remains to be decided whether the retrieved information, now available to consciousness, corresponds to the target episode or to another episode. This necessarily requires a comparison process between the retrieved information and some kind of representation of the target episode. More specifically, this monitoring process will be based on the fact that the retrieved information contains or does not contain some features which seem to be characteristic of the target episode. This supposes the person to be able to reinstate the contextual information associated with the episode. It remains also to be decided whether this information corresponds to an episode that has really been experienced or corresponds to a dream, a wish, a thought, or any other product of imagination. To decide, the person will have to take into consideration the diagnostic value of different characteristics associated with the accessed memory, such as perceptual vividness, semantic details, and so on. The person will also set a decision criterion from these characteristics. Besides, a retrieval cue may lead to the retrieval of an episode different from the target episode: a difficulty to match the information contained in the cue and the memory trace then arises. In such a case, the person will have to build a more precise description of the characteristics of the target episode (a process of focusing according to Norman & Schacter, 1996; Schacter et al., 1998). The concept of focusing refers to the fact that a retrieval cue should include a maximal number of features which are being characteristic of the target trace but not of competing traces. This focusing process could involve both a process of activation of the target trace and a process of inhibition of inappropriate representations.

To sum up, three stages of active retrieval of an episodic information are generally distinguished. During the first step, the retrieval is specified, i.e. a description of the target memory is built and verification criteria are set. The second step involves a matching between the description of the target memory with stored memories. Finally, any retrieved memory that matches the target memory in a satisfactory way is evaluated with respect to the verification criteria set during the first step. Moreover, the initial description may be modified if further information becomes available during the retrieval cycle.

There remain nevertheless unanswered questions regarding both the specificity of the memory operations which are impaired after a frontal lesion, and the exclusive relationship between these operations and the frontal lobe areas (Mayes & Daum, 1997). One could first ask whether the impairments following a frontal lesion are qualitatively different, i.e. whether they actually affect distinct processes. For example, Shallice (1988) suggested that the Supervisory Attentional System (SAS) is responsible for the strategic encoding and retrieval processes, as well as the monitoring of the retrieved information. The frontal lobes are held to implement the functions of this supervisory system. These different processes (strategic encoding and retrieval, monitoring of retrieved information) may be selectively impaired by a frontal lesion. More specifically, a disorder affecting the monitoring of retrieved information should lead to a specific impairment of recognition (i.e., the patient is no longer able to evaluate items as being old or new) while the performance in a recall task should not be affected (although one might expect a higher rate of intrusions). A monitoring disorder should also elicit confabulations as well as difficulties to assess the frequency of the presented items. A disturbed use of encoding strategies, retrieval strategies or both should, on the contrary, lead to deficits of anterograde free recall. However, only a selective deficit affecting retrieval strategies would lead to an impairment of the recall of information learnt before the onset of the brain lesion. Norman and Schacter (1996; see also Schacter et al., 1998) also share the idea that frontal lobes play a important role in strategic retrieval and in monitoring retrieved information. However, they consider that these two processes are dependent on reinstating (in a top-down way) contextual information associated with the target episode, and thus, that it is not necessary to assign them to separate brain structures, nor to expect dissociations between deficits of strategic retrieval and deficits in monitoring retrieved information.

In other respects, there are studies suggesting that some memory deficits following a frontal lesion could be domain-specific. In that perspective, Norman and Schacter (1996) suggest that a lesion affecting the ventromedial frontal areas (a lesion which frequently produces confabulations and false recognitions) would lead to a global deficit affecting the creation of focused representations of the target episode. On the other hand, dorsolateral frontal lesions would impair the ability to incorporate certain kinds of constraints in the representations of the target episode (e.g., the visuo-spatial constraints in patients with a right dorsolateral lesion).

Moreover, one can ask if the memory deficits following a frontal lesion specifically impair memory functioning or if they are secondary to more general disorders affecting the strategic organisation of the cognitive processes. In that respect, it should be noted that a number of frontal areas involved in the episodic memory functioning are also involved in working memory processes (Owen, 2000; Wagner, 1999). Another question is to know whether the link between some memory impairments and the frontal areas is exclusive or not.

In other words, could the memory deficits observed after frontal lesions be also observed after a lesion affecting other brain regions? The consequences of these non-frontal lesions could be similar to those of frontal lesions either because the non-frontal regions belong to a network including the frontal regions or because they contribute to some basic functions which underlie the memory task in question.

In order to answer these different questions, it will be necessary to identify more precisely the operations involved in the recollection and verification processes. From a neuropsychological point of view, future research should also investigate whether lesions affecting different frontal cortex areas lead to multiple dissociations of impairments. Finally, functional brain imaging may also contribute to identify the specific contribution of frontal areas to episodic memory functioning.

Brain imaging of episodic memory

A large set of studies using functional brain imaging were carried out in order to identify the neural correlates of the subprocesses that are involved in episodic memory (see Buckner, Kelley, & Petersen, 1999; Nyberg et al., 2000; Nyberg & Cabeza, 2000). Large-scale networks of brain regions, including distinct regions within the prefrontal cortex, have been found to be engaged in episodic memory operations. Consistent observations indicated that left prefrontal cortex regions appear to be preferentially involved in encoding episodic information (along with semantic retrieval), while right prefrontal cortex regions (namely a region in the right anterior prefrontal cortex: Brodman Area [BA] 10) are preferentially involved in the retrieval of episodic information and in monitoring operations (the hemispheric encoding/retrieval asymmetry, HERA, model; Nyberg, Cabeza, & Tulving, 1996). Some findings (e.g., Dolan & Fletcher, 1997) also suggest that two processes are involved in encoding: novelty assessment, partly mediated by hippocampal regions, and meaning-based encoding operations, partly mediated by left frontal lobes. However, other studies (see Buckner, Kelley, & Petersen, 1999) showed that multiple left and right frontal regions may participate in encoding, depending on the kind of information being memorized (e.g., words, pictures scenes, or faces).

Concerning retrieval, Lepage, Ghaffar, Nyberg, and Tulving (2000) point to the necessity for a revision of the retrieval-related aspects of the HERA model and propose that the typically observed left/right asymmetry of retrieval activations seems to be mostly attributable to the maintenance of episodic memory retrieval mode (REMO). Furthermore, Nyberg et al. (2000) indicate that distinct (left and right) prefrontal regions may mediate retrieval mode and retrieval success. It should also be noted that a recent analysis of functional connectivity suggests that activity in certain right prefrontal areas can reflect either retrieval mode or retrieval success, depending on their functional relations with other regions (McIntosh, Nyberg, Bookstein, & Tulving, 1997). In addition, Nolde, Johnson, and Raye (1998) also identify conditions in which left prefrontal regions are activated during episodic retrieval. They proposed a model of 'cortical asymmetry for reflective activity' (CARA) according to which right and left prefrontal cortices are differentially activated as a function of the relative complexity of retrieval. The right prefrontal cortex would be activated in relatively simple episodic memory retrieval situations, i.e. in forced recognition tasks. On the contrary, the left prefrontal cortex would be activated when retrieval implies more controlled (reflective) processes, such as initiation of self-cueing, or a detailed verification of the retrieved information. From a more general perspective, it appears that episodic memory is mediated by large-scale neural interactions between material-specific and process-specific neural substrates of episodic encoding and retrieval (including prefrontal and posterior brain regions). More recently, Raye, Johnson, Mitchell, Nolde, and D'Esposito (2000) confirm that increments in reflective processing complexity are likely to produce increases in prefrontal cortex activation, but the "localisation" of this increased activity appears to depend on the level of involvement of each hemisphere in the baseline task and the specific cognitive processes in the complex task. It should, however, be mentioned that according to Rugg and Wilding (2000), few studies have used designs that permit the different kinds of retrieval processes, and their neural correlates, to be independently identified

Even if some imagery data are consistent with a functional heterogeneity of the prefrontal cortex, some prefrontal regions also seem to be part of more than one network subserving different memory abilities. This latter statement is true for both the episodic and working memory systems.

Brain imaging of working memory

Working memory refers to a limited capacity system responsible for the temporary storage and processing of information while cognitive tasks are performed. The multi-component model proposed by Alan Baddeley and Graham Hitch (Baddeley, 1986; Baddeley & Hitch, 1974) represents the most extensively investigated and the best articulated theoretical account of working memory. It consists of a modality-free controlling central executive which is aided by two slave systems ensuring temporary maintenance of verbal and visuospatial information: the phonological loop (composed of a phonological store and an articulatory rehearsal system) and the visuospatial sketchpad.

The core of the working memory model is the central executive. It is assumed to be an attentional control system responsible for strategy selection and for control and coordination of the various processes involved in short-term storage and more general processing tasks. Baddeley (1986) has suggested that the Supervisory Attentional System (SAS) component of the attentional control of action model proposed by Norman and Shallice (1986) might be an adequate approximation of the central executive system. Norman and Shallice (1986)'s model distinguishes two control-to-action mechanisms. The first one, called contention scheduling, is involved in the routine situations in which actions are automatically triggered. The second one, called the Supervisory Attentional System (SAS), is a separate mechanism at the highest level of control of action, coping with novelty. This mechanism is required in situations where the routine selection of actions is unsatisfactory, and is involved in the genesis of plans and willed actions. Additionally, the central executive or the SAS is conceived as carrying out a variety of processes (Baddeley, 1996; Shallice, 1988, 1994). Empirically, it is now also becoming apparent from neuropsychological studies that particular impairments, within the general set of SAS or central executive operations, can be isolated (e.g., Eslinger & Damasio, 1985; Shallice & Burgess, 1993, 1996; Stuss, Shallice, Alexander, & Picton, 1995).

Recently, Miyake, Friedman, Emerson, Witzki, and Howerter (2000) administered a set of executive tasks to a large group of young participants in order to examine the separability of three often postulated executive functions (updating and monitoring of working memory contents, inhibition of prepotent responses, and shifting between mental sets or tasks). Confirmatory factor analysis indicated that these three executive functions are moderately correlated with one another, but are clearly separable, thus indicating both unity and diversity of executive functions. Moreover, structural equation modeling suggests that the executive tasks often used in cognitive and neuropsychological studies are not completely homogeneous in the sense that the three executive functions isolated (updating, inhibition, and shifting) contribute differentially to performance on complex executive tasks. For example, performance on the Wisconsin Card Sorting Test was related most strongly to the shifting function but performance on the Tower of Hanoi to inhibition processes. The only complex executive task that did not relate clearly to the three target executive functions was the dual task. This suggests the possibility that the simultaneous coordination of multiple tasks is an ability that is somewhat distinct from the three executive functions explored in this study. According to Miyake et al., at least two explanations may be proposed to take into account the intercorrelations among the three target executive functions. First, all the tasks used in the study require the maintenance of goal and context information in working memory. In other words, they require what Engle, Kane, and Rettinger (1999) call a "controlled attention" capacity, which is a domain-free attentional capacity to actively maintain or suppress working memory representations. Another interpretation is that the three executive functions involve an inhibitory capacity, which is considered by certain authors as a basic unit of working memory or executive functioning (e.g., Dempster & Corkill, 1999; Zacks & Hasher, 1994). An inhibition control mechanism is also at the centre of Shimamura (2000)'s view suggesting that many aspects of executive control, such as selecting, maintaining, updating, and rerouting information processing, could be interpreted as aspects of dynamic filtering, such as filter selection, filter persistence, and filter switching.

Numerous functional neuroimaging studies have investigated the neural substrates of the different subcomponents of working memory (for a review, see Collette & Van der Linden, 2000). With regard to the phonological loop, a network of left-sided areas (including posterior parietal, opercular, and premotor frontal regions) was found by various authors (e.g., Paulesu, Frith, & Frackowiak, 1993; Salmon et al., 1996). More specifically, the phonological store has been associated with activations in parietal regions and the articulatory rehearsal system with activations in Broca's area. Concerning the visuospatial sketchpad, maintenance of object information has been associated with (mainly left-lateralized) activation of occipito-temporal and inferior prefrontal regions and maintenance of spatial information with (mainly right-lateralized) activation of occipito-parietal and superior prefrontal regions (see Smith, 2000). Finally, central executive functions are typically associated with activations in prefrontal regions: several studies (e.g., Collette, Salmon et al., 1999; D'Esposito, Detre, Alsop, Shin, Atlas, & Grossman, 1995; Van der Linden et al., 1999) showed that some executive functions including working memory updating, monitoring and manipulation of information in working memory, and dual task coordination activate the mid-dorsolateral frontal cortex (BA 9 and 46) and frontopolar cortex (BA 10), sometimes along with posterior (mainly parietal) regions. It should be noted that activation of other frontal regions, especially ventrolateral regions (BA 45 and 47), have also been observed during verbal or spatial working memory tasks (e.g., Owen, Doyon, Petrides, & Evans, 1996; Owen, Lee, & Williams, 2000).

With regard to Miyake's suggestion that dual-task coordination is relatively not related to shifting processes, it must be noted that other authors (e.g., Shimamura, 2000) consider, on the contrary, that the capacity to continuously shift between cognitive processes can be assessed by dual-task performance. In that context, D'Esposito et al. (1995) asked participants to perform a semantic judgement task and a visuo-spatial task either separately or simultaneously. Significant prefrontal activation (BA 9 and 46) was observed when participants performed the two tasks simultaneously but not when they performed them separately. Other authors (e.g., Adcock, Constable, Gore, & Goldman-Rakic, 2000) have nevertheless demonstrated that dual-task coordination is not dependent upon a specific prefrontal area but rather involves the interplay of various specialized information-processing systems already involved in the realization of the single-task components.

However that may be, shifting processes are also considered to be involved in tasks requiring the alternative movement of the attentional focus from one stimulus attribute to another. Although relatively few studies were interested by the neural substrates of these shifting processes, both neuroimaging studies and data from brain-damaged patients suggest that the prefrontal cortex would be involved. Ragland et al. (1997; see also Faith-Berman et al., 1995) have obtained neuroimaging data suggesting that the prefrontal cortex plays a role in the switching between different dimensions of a stimulus. However, the multi-compound aspect of the task used in these studies (the Wisconsin Card Sorting Test) did not permit to associate a specific cerebral area with the shifting process. Finally, the exploration of brain-damaged patients is also in agreement with the hypothesis of a frontal involvement during shifting processes. Dunbar and Sussman (1995) assessed patients with frontal lobe lesions on a Stroop-like picture-word paradigm. Although frontal patients did not exhibit greater interference in comparison to controls, the patients were particularly slow in a shifting condition in which they were cued at the beginning of each trial to either name the picture or read the word. Moreover, Duncan, Emslie, Williams, and Johnson (1996) demonstrated that these patients exhibited difficulties in switching between the different ways to process a stimulus (i.e., to report stimuli presented alternatively in a left or right stream). More generally, there still exist some uncertainties concerning the relationships between task-shifting and dual-task coordination (e.g., Hartley & Little, 2000) as well as between task-shifting and stimulus-shifting. In addition, the relative contribution of top-down (deliberate) mechanisms and bottom-up processes in the switch cost (i.e., in how task-switching affects performance) is not completely understood (Pashler, Johnston, & Ruthruff, 2001).

Consequently, the exploration of the neural substrates involved in shifting and dual-task coordination will be dependent upon a better specification of these control processes.

The relationships between working memory and episodic memory

The results summarized above indicate that working memory is based on distributed networks involving interactions between prefrontal and posterior regions. Different theoretical frameworks have been proposed in order to understand the role of the prefrontal cortex in working memory (see Owen et al., 2000; Owen, 2000; Postle & D'Esposito, 2000). A first type of model suggests that the lateral frontal cortex is organized according to the nature of the material being processed, with dorsolateral frontal regions being principally concerned with spatial information, whereas the ventrolateral frontal regions are related with nonspatial information (e.g., Courtney, Ungerlieder, Keil, & Haxby, 1996, 1997). However, there is now converging evidence indicating that working memory processes within the dorsolateral and ventrolateral frontal cortex are organized according to the type of processing required rather than according to the nature of the information being processed. For example, Owen et al. (2000) showed that varying the executive requirements of a simple verbal working memory task (forward vs. backward digit span) induces distinct contributions of the lateral frontal cortex: during forward digit span, activation was observed within the mid-ventrolateral cortex, but not within the mid-dorsolateral cortex; during backward digit span, activation was observed in both regions (for similar results with spatial span tasks, see Owen, Evans, & Petrides, 1996). In the same vein, it has been demonstrated that performance on visual spatial and visual nonspatial working memory tasks involved identical regions of the lateral frontal cortex when all the factors unrelated to the nature of the material were controlled (Owen, Stern, Look, Tracey, Rosen, & Petrides, 1998).

Furthermore, Owen (2000; see also Owen et al., 2000) suggests that the mid-dorsolateral frontal cortex will be recruited when active manipulation or "monitoring" of information is required. In contrast, the ventrolateral cortex will be related to a relatively straightforward mapping of stimulus to responses, such as that which occurs in the digit span and spatial span tasks. In addition, considering the fact that episodic memory processes require some prefrontal areas that are also associated with various working memory processes, he suggests that a fruitful approach may be to consider that the various processes involved in working memory, episodic memory encoding and retrieval, and other executive functions are drawn from a single set of underlying components, although they may be differentially represented in different tasks. The episodic memory study conducted by Fletcher, Shallice, Frith, Frakowiak, and Dolan (1998) may illustrate this approach. The authors reported activation in the mid-ventrolateral frontal cortex during a paired-associates task that required the participant to retrieve previously learned category exemplars in response to a series of category names. In addition, activation in the mid-dorsolateral frontal cortex was observed during a condition that requires the participant to freely recall items from a previously learned list. According to Owen (2000), a general role for the ventrolateral frontal cortex in memory would be to trigger active low-level encoding strategies, such as rehearsal, and to initiate explicit retrieval of information from long-term memory. In contrast, the dorsolateral frontal cortex would be activated in memory situations (such as free recall) that require to monitor responses made and information assimilated earlier in each trial.

More recently, Duncan and Owen (2000) showed that a specific frontal-lobe network including the mid-dorsolateral, mid-ventrolateral and dorsal anterior cingulate cortex is consistently associated with a broad range of cognitive demands, including aspects of perception, response selection, working memory, episodic memory, and problem solving. Much of the remainder of frontal cortex, including most of the medial and orbital regions, is largely insensitive to these demands. Clearly, the future challenge is to identify how these regions work together to meet such diverse cognitive problems. In addition, Owen (2000; see also Duncan & Owen, 2000) recognized that this theoretical framework does not rule out the possibility of a finer specialization within this network and, for example, that some functional differentiation based on the nature of the material might also exist within these particular frontal cortical regions.

In this direction, Postle and D'Esposito (2000), evaluating the models of organization of working memory function in the frontal cortex with event-related fMRI, suggest that organization-by-process models and organization-by-stimulus-domain are orthogonal and that the organization of working memory function in the prefrontal cortex reflects principles drawn from both. More specifically, they propose that the processes supporting manipulation of information held in working memory are largely confined to the dorsolateral prefrontal cortex, bilaterally; processes related to working memory maintenance of verbal information are left lateralized in the ventrolateral prefrontal cortex (BA 44 and 45), but the dorsolateral prefrontal cortex is also activated by these processes to an extent comparable to the ventrolateral prefrontal cortex; processes supporting working memory maintenance of spatial and nonspatial visual material are also broadly distributed, but they are dissociated in the anterior ventrolateral area 47, where object maintenance is preferentially left lateralized, and spatial maintenance is preferentially right lateralized.

Finally, Wagner (1999) also reviewed recent PET and fMRI studies and demonstrated a contribution of similar prefrontal regions to episodic and working memory in humans. On that basis, the author hypothesized that prefrontal activation during episodic memory reflects the recruitment of specific working memory processes. More precisely, the activity in inferior prefrontal areas would reflect the recruitment of material-specific working memory processes that support access to, maintenance of, and evaluation of specific event attributes during the realization of episodic memory tasks. For example, the left anterior part of the inferior prefrontal cortex (BA 47) would mediate semantic working memory processes, the posterior inferior part (BA 44/6) phonological working memory processes while visuospatial working processing would be dependent on the right inferior frontal cortex (BA 44/6 and BA 45). Otherwise, studies of episodic memory suggest that activation in right dorsolateral (BA 46/9) and anterior prefrontal (BA 10) cortices is material independent and is modulated by episodic retrieval but not episodic encoding. These activations were interpreted as reflecting the recruitment of material-independent working memory operations that support the manipulation of the contents of episodic memory irrespective of the nature of the material being processed. An example of such working memory processes could be the monitoring and manipulation of the products of retrieval from long-term memory (Wagner et al., 1998).

To summarize, recent PET and fMRI studies have shown that different prefrontal areas are involved in different working memory and episodic processes. More specifically, there now exists converging evidence that some episodic memory processes such as, for example, retrieval and evaluation of information, are mediated by working memory mechanisms, which are either material specific or process specific; these mechanisms depend on different prefrontal regions which could be involved in a complex frontal lobe network including the dorsolateral and ventrolateral frontal cortex as well as, probably, the anterior cingulate cortex. Future research will obviously be necessary in order to reach a more integrated view of the role of these frontal regions in both working memory and episodic memory processes. Moreover, further insights about the role of the human prefrontal cortex in episodic memory, working memory, and executive functions are likely to emerge from the examination of two other cognitive processes: inhibitory control and binding processes.

Binding processes

Episodic memory enables to create representations of personal events in which a central information is associated to contextual details. The richness of the representation can be a useful trump when the episode must be retrieved. Contextual details can serve as cues to help remembering the central information, or the origin of this information (Johnson, Hashtroudi, & Lindsay, 1993). However, this can only be done if the different contextual information is bound to the central information. In other words, temporal and spatial information, affective conditions, cognitive operations, physical characteristics of objects, modality of presentation, among others, must be integrated into a coherent representation. In this sense, binding is the most crucial process involved in episodic memory.

An important distinction has to be made between incidental and intentional binding. Hasher and Zacks (1979) 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 information (i.e., spatial context or frequency of occurrence) are best processed automatically (i.e., incidentally), while others are processed in an effortful mode (i.e., 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 information and its context benefits more from one mode of encoding than from the other. In a recent study, using a procedure developed by Chalfonte and Johnson (1996), Marczewski, Van der Linden, and Martin (2000) showed that age had no effect on the binding of objects and locations, when strategic processes that can be involved in binding are taken into account. Indeed, older adults performed exactly at the same level as the young in the incidental binding condition, in which no strategic encoding was promoted. However, the intentional encoding of the relationship between objects and locations led young adults to a better recollection of the precise conditions of encoding. As observed by Ellis (1990), the natural encoding mode of spatial context is automatic, but in young adults, adding strategic processes may help. In other words, even if spatial information is preferentially processed in an automatic mode, there is no logical reason to think that focusing attention or initiating strategies could not help. Notably, processing more and processing better should be discriminated. Marczewski et al.'s results show that intention did not lead to a greater number of locations encoded and recognized in young adults, but to a more detailed representation of the encoding situation. In addition, they suggested that the intentional binding deficit observed in aging for objects and locations in long-term memory was partly due to a loss of efficiency in translating the spatial information into a verbal code that normally improves the encoding. Finally, Mitchell, Johnson, Raye, Mather, and D'Esposito (in press) have recently suggested that the impairment of elderly adults in binding objects and locations intentionally is not limited to long-term memory, but rather, is related originally to a deficit in working memory.

In order to capture a range of phenomena which are not readily explained by the actual model of working memory, Baddeley (2000) recently proposed the existence of a supplementary component, the episodic buffer. The episodic buffer, which is involved in binding processes, represents a limited capacity system providing temporary storage of information held in a multi-modal code, capable of binding information from the subsidiary slaves systems and from long-term memory into a unitary representation by means of a multidimensional code. For Baddeley, this concept of an episodic buffer resembles Tulving's concept of episodic memory (Tulving, 1989). However, it differs in that it is a short-term system that is linked to long-term memory but not dependent on it. In that sense, the existence of similar binding processes could be postulated in short-term and long-term memory tasks. At the present time, no studies have compared directly the binding processes involved in these two types of tasks.

Two recent imagery studies have been conducted in order to explore the neural correlates of binding processes in working memory. Prabhakaran, Narayanan, Zhao, and Gabrieli (2000) used fMRI to identify brain regions preferentially involved in maintaining integrated versus unintegrated spatial and verbal information in working memory. In the integrated condition, four letters were displayed in four locations, in such a manner that verbal and spatial information were bound together. In the unintegrated scan, the four letters were presented centrally and separately from the four indicated locations; thus verbal and spatial information was separate. After a retention interval, participants had to judge whether both the letter and the location had been shown in the previous display. Results indicate that the right middle and superior frontal gyri (BA 9, 10, 46) were more involved in the maintenance of integrated information, while the maintenance of unintegrated (spatial and verbal) information required a greater involvement of the posterior cerebral areas (bilateral parietal, temporal and cerebellar regions). Since participants were more accurate and faster in the bound than in the separate condition, we can suppose that prefrontal activation reflected the binding process in working-memory, rather than working-memory load or task difficulty. The greater activity observed in posterior cerebral areas (classically attributed to the storage of information in working memory) during the unintegrated conditions suggests that more neural resources are required when maintaining separate information than bound information. Thus, integration may provide for efficient working-memory representations.

In another study, Mitchell, Johnson, Raye, and D'Esposito (2000) administered a slightly different working memory task to young and older adults in order to distinguish neural deficits from age-related deficits in feature binding. In this task, each trial consisted of three grids presented sequentially, each grid containing a different object in a different location. Participants were instructed before the trial to remember object, or location, or both. For young, but not older adults, there was greater activation in the left anterior hippocampus and right medial frontal gyrus (BA 10, an area included in the Prabhakaran et al. integration area) when participants had to remember objects together with their location than on trials in which participants were told to remember only which objects or only which locations occurred. Moreover, both the anterior cingulated (BA 24/32) and left precentral gyrus/premotor cortex (BA 6) were also more activated in the binding condition.

A few functional imagery studies have tried to determine the cerebral areas associated with the retrieval of contextual information, mainly the temporal or spatial context. Spatial context retrieval has been associated with the inferior parietal cortex (e.g., Köhler, Moscovitch, Winocur, Houle, & McIntosh, 1998) and the left frontal cortex (Nyberg, McIntosh, Cabeza, Habib, Houle, & Tulving, 1996). Temporal context retrieval has been associated with the anterior cingulated cortex (Nyberg, McIntosh et al., 1996) and the parietal and dorsal prefrontal cortices (Cabeza et al., 1997). However, none of these studies have specifically taken into account the encoding conditions of the contextual information.

In a recent PET study, Lekeu et al. (2000) directly contrasted the conditions of contextual incidental and intentional encoding. More precisely, these authors explored the brain regions involved in the episodic recognition of items (words) bound to contextual colour features. Colour was chosen as contextual information because behavioural studies had demonstrated that unrelated colour contexts were best encoded intentionally rather than incidentally. Results indicated differential effects of the encoding mode of the contextual information: an activation of the left middle frontal gyrus (BA 46) and left superior parietal lobule (BA 7) was observed in the incidental binding condition, while the intentional binding condition was associated with increases of activity in the right superior frontal gyrus (BA 9) and the left middle frontal gyrus (BA 46). Thus, this study clearly demonstrates the intervention of different cerebral areas in episodic retrieval according to the type of contextual encoding.

In summary, cognitive studies have demonstrated the existence of two binding processes, with contextual information being processed either in an automatic or in an effortful mode. Functional imagery studies of episodic memory have confirmed these data, showing that the recognition of the bound features was associated with different cerebral areas in relation to the mode of encoding (incidental or intentional) of the contextual information (Lekeu et al., 2000). The experiments which explored the intentional binding processes in working memory (Mitchell et al., 2000; Prabhakaran et al., 2000) used only spatial contextual information; these studies showed that the spatial binding process in working memory is associated to right frontal areas, whereas this binding process was linked to left frontal areas during episodic tasks (Nyberg, McIntosh et al., 1996). In order to get a better understanding of the exact relationships between prefrontal areas, working memory and episodic memory binding processes, further studies will be necessary. In that context, two research domains appear particularly fruitful: the direct comparison (both at a cognitive and neuroanatomical level) of the binding processes in working memory and episodic memory for the same kind of contextual information, and the comparison of encoding and retrieval processes for different contextual information in the same (working or episodic) memory domain.

Inhibition, working memory, and episodic memory

It is generally considered that inhibitory control constitutes an important executive function (Baddeley, 1986; Norman & Shallice, 1986). Numerous clinical observations of patients with frontal lesions suggested that the prefrontal cortex plays a central role in the process of inhibitory control, while other studies did not reveal impaired performance in these patients on inhibition tasks (for a review, see Andrès, Van der Linden, Collette, Le Gall, 2000). Inhibition control was also explored with functional imaging studies by using different paradigms classically described as assessing inhibitory functions, such as the Stroop task, the Wisconsin Card Sorting Test, and the go/no-go paradigms (e.g., Konishi, Nakajima, Uchida, Kikyo, Kameyama, & Miyashita, 1999; Pardo, Pardo, Janer, & Raichle, 1990). The results obtained in these studies showed activations involving not only bilateral prefrontal areas, but also posterior regions and subcortical structures (for a review, see Collette, Delrue, Van der Linden, & Salmon, 2001). Moreover, there exists an important heterogeneity in the cerebral areas activated by the various inhibition tasks, and also within the different studies using variants of a same paradigm. However, some cerebral areas are consistently found in most studies, especially the anterior cingulate gyrus (BA 24/32), the inferior frontal area (BA 45), and the middle frontal gyrus (BA 10).

It is important to note that prefrontal activation was also linked to inhibition processes in episodic memory. Schnider, Treyer and Buck (2000) explored the cerebral areas associated with the active inhibition of currently irrelevant memories. They administered a continuous recognition task in which participants saw pictures and were requested to indicate picture recurrence within the test run (first trial). After the first trial, additional runs were presented with the same pictures in a different order. Again, participants had to indicate picture recurrence in the current run. In these trials, all items were familiar since they had been presented previously. Thus, the performance on these trials required making the distinction between the events in the present run as opposed to the previous run. The comparison of the subsequent trials with the first one showed a specific activity in the posterior orbitofrontal area. Consequently, the authors attributed to this area a role in the inhibition of currently irrelevant memories onto ongoing thought.

However, at the present time, the specific role of the cerebral areas consistently found during the realization of various inhibition tasks is not really clear. Indeed, the tasks used are generally complex, multi-compound and involve numerous cognitive processes other than inhibition. Moreover, another problem related to the exploration of the neural substrates of inhibitory processes concerns the lack of theoretical specification of that concept. The concept of inhibition cannot be considered as unitary and refers probably to very different mechanisms; at the present time, the relationships between these various inhibitory mechanisms are not clearly established (Connely & Hasher, 1993; Kieley & Hartley, 1997; McDowd, 1997; Stolzfus, Hasher, Zacks, Ulivi, & Goldstein, 1993).

Conclusion

The study of the relationships between memory processes and executive functions has much benefited from neuroimaging paradigms. These studies have demonstrated that similar prefrontal areas are involved in a large range of tasks requiring working memory processes, retrieval and encoding processes in long-term memory as well as executive processes. These data could indicate that quite different tasks require the intervention of similar cognitive mechanisms (e.g., the "inhibition" executive function intervenes in episodic memory tasks to suppress the interference of currently irrelevant encoded information). However, at present, neuroimaging techniques have not permitted to determine what exactly the functional interactions between these prefrontal areas are, nor their interactions with posterior cerebral regions. Indeed, one hypothesis could be that, even if similar cerebral areas underline these various cognitive processes, the relationships between the regions are slightly different from one cognitive domain to another. Further neuroimaging studies with appropriate statistical techniques will be obviously necessary to answer that question.

The exploration of cognitive impairment in Alzheimer's disease also constitutes an alternative approach to the study of the relationships between long-term memory and working memory. Indeed, recent data suggest that the impairment of verbal span performance in these patients would not be due to a working memory deficit, but rather to a less efficient transfer of information stored in long-term memory to the phonological loop of working memory (Collette, Van der Linden, Bechet, & Salmon, 1999). Moreover, there also exists neuroimaging evidence that the higher-level cognitive deficits in these patients are due to a decrease of the functional connectivity between cerebral areas: when performance on a series of executive tasks was assessed in a group of Alzheimer patients with cerebral hypometabolism restricted to posterior areas and a group of patients with hypometabolism in anterior and posterior cerebral areas, no difference was found between the two groups, suggesting that executive dysfunction observed in Alzheimer's disease could be due to a (partial) disconnection between anterior and posterior cortical areas (Collette et al., 2001), leading to a less efficient transfer of information between these areas (see also Morris, 1994a, 1994b, for a similar hypothesis).

In that context, the simultaneous exploration of working memory, long-term memory and executive processes with tasks specifically designed to measure intra- and inter-hemispheric disconnection should be particularly fruitful in Alzheimer's disease. Indeed, the presence of associations and dissociations in the performance on tasks assessing different cognitive functions will give some information about the relationships between these functions. Moreover, a correlation analysis between task performance and distribution of the cerebral metabolism would indicate whether the same (prefrontal) cerebral areas underlie impairments of different cognitive processes (e.g., retrieval in episodic memory and inhibition).

In conclusion, this review demonstrates that our knowledge concerning the functioning of different high-level cognitive processes and their cerebral substrates has dramatically increased in the last few years. However, it appears that one important limitation of these studies comes from the fact that most of them were centred upon one specific domain. A more integrated comprehension of the relationship between executive functions and memory processes will probably come from studies aimed at exploring the connections between different cognitive domains – a research area in which neuroimaging paradigms seem to be particularly fruitful.

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