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Abstract

After a brief description of the "diseases of memory" which have made the greatest contribution to theoretical developments in the past years, we turn our attention to the most important concepts to have arisen from the dissociations brought to light in different neuropsychological syndromes. This is followed by a critical review of the tasks currently used to assess each memory system. We then describe the monohierarchical model proposed by E. Tulving (1995), together with other recent concepts, notably Baddeley's model of working memory with its latest component, the *episodic buffer*. Lastly, we attempt to reconcile these models with several other theoretical propositions, which we have linked together in a macromodel - the Memory NEo-Structural Inter-Systemic model (MNESIS).
Key words: episodic memory, working memory, semantic memory, memory tasks, memory models.

Introduction

A plural view of memory is certainly the most satisfactory concept, when it comes to giving account of current neuropsychological knowledge and forming clear, heuristic working hypotheses. These hypotheses focus on the rules governing the working of memory systems, their organization and their interrelations. In this article, after a brief description of the "diseases of memory" and the most important concepts in memory research, we attempt to reconcile several recent theoretical propositions, which we have linked together in a macromodel - the *Memory NEo-Structural Inter-Systemic* model (MNESIS). While MNESIS deliberately goes along with multisystem concepts, it also puts forward hypotheses about the interrelations between these systems, which may each be based on an individual micromodel.

Brief Review of Disease of Memory

The main dissociations brought to light during structured neuropsychological examinations were first discovered in *permanent amnesic syndromes*, notably bilateral hippocampal amnesic syndrome (HM being the archetypal case; Scoville & Milner, 1957) and Korsakoff's syndrome, the most frequent form of diencephalic amnesia (Kopelman, 2002). In both cases, these syndromes combine anterograde amnesia and retrograde amnesia, though numerous memory capabilities are preserved. It is on these dissociations between disturbed and preserved memory capabilities that multisystem concepts of memory are based. Also of great interest are *transient global amnesias* that affect individuals who otherwise enjoy good health and do not have time to adjust to their disorder and develop compensatory mechanisms (Guillery-Girard *et al.*, 2004, Quinette, Guillery-Girard, Dayan, *et al.*, 2006). Over the last few years, amnesic syndromes in children, known as *developmental amnesias*, have come to occupy a unique place in the neuropsychology of memory (Vargha-Khadem *et al.*, 1997; Martins *et al.*, 2006). The description of this new syndrome has revived several theoretical debates, such as the one concerning the acquisition of semantic knowledge without episodic memories and the role of the hippocampal region in different memory systems (see Squire & Alvarez, 1995 and Nadel & Moscovitch, 1997, for contradictory models, and Viard *et al.*, 2007 for recent imaging findings). With a few exceptions, the neuropsychology of memory used to be restricted to organic pathologies (i.e. with cerebral lesions). Over the last few years, numerous cases of *psychogenic (or functional) amnesias* have been observed, and these observations are now contributing fully to the development of theoretical models of memory (Markowitsch *et al.*, 1999; Piolino *et al*, 2005). Although the profiles of psychogenic and organic amnesia bear a close resemblance to each other, distinguishing features have been identified, based on clear criteria (Kapur, 1999, Kopelman, 2002). Nevertheless, some investigators have pointed out the frequent concomitance of neurological and psychological problems, especially in cases with mild concussion accompanied by profound amnesia (Kopelman & Kapur, 2001). The study of memory has also been extended to various *psychiatric pathologies* (such as schizophrenia and depression), and this highly active and innovative field of research will no doubt yield elements which will increase our understanding of the relations between memory and affect (Danion *et al.*, 2005). More specifically, this research provides indications as to how memory systems and representations are constructed (and deconstructed) in the course of an individual's development. This issue is extremely important, as it tackles the central problem of relations between memory and the self's aspirations (see for example, Conway, Singer, & Tagini, 2004).

Lastly, an important topic of research in the last twenty years has concerned the growing incidence of *neurodegenerative diseases*. Concepts and models in the neuropsychology of memory were initially applied to various dementias from a purely descriptive viewpoint. However, this work soon revealed profiles of new disorders, sometimes even revealing double dissociations between different dementias or between dementias and amnesic syndromes. Because it is so common, *Alzheimer's disease* is the most widely-studied pathology, and cognitive neuropsychology has shown that deficits can be highly selective, at least in the early stages of the disease. The neuropsychology of dementias has been conducted into other diseases, not least the group of *fronto-subcortical dementias* (such as Huntington's disease; Albert, 2005) and, more recently, *frontotemporal dementias* (see for example Matuszewski *et al.*, 2006 for an investigation of autobiographical memory). Among the latter, a temporal variant has been identified, known as *semantic dementia*. This is a form of lobar degeneration which predominantly affects the temporal lobe (Desgranges et al., in press) and results in the virtually isolated impairment of semantic memory - a situation rarely encountered in other pathologies (Snowden *et al.*, 1989; Hodges, Patterson, Oxbury, & Funnell,1992).

Although neurodegenerative diseases, characterized by diffuse and evolutive lesions, may seem at first sight to be poor pathological models of memory, dementias can actually contribute new theoretical elements at both the cognitive and neuroanatomical levels. New methods of anatomical and functional imaging allow us to view the dysfunctioning regions of the brain at the root of the neuropsychological disorders in these diseases (Desgranges, Baron, de la Sayette, *et al.*, 1998; Desgranges *et al.*, 2002; Eustache, Desgranges, Giffard, de la Sayette, & Baron, 2001; Eustache *et al.*, 2004; Rauchs *et al.*, 2007). Similarly, the changing nature of the cognitive deficits, which makes it difficult to take the sort of static snapshot we can of other neuropsychological syndromes, allows us instead to observe the dynamics of memory processes and their interrelations. Longitudinal studies, regrettably still few and far between, can prove invaluable in helping us to understand certain pathological phenomena (see, for example, Giffard *et al.*, 2002, for semantic priming). Memory impairment, the most important aspect of Alzheimer's disease, has even been detected prior to the onset of dementia. Studies looking for ways of improving early diagnosis are therefore focusing on patients who display Mild Cognitive Impairment (MCI; Petersen *et al.*, 2001; Dubois & Albert, 2004; Nestor, Scheltens, and Hodges, 2004), the aim being to identify those who will go on to develop dementia in the months that follow. Research combining neuropsychological investigations and neuroimaging studies looks extremely promising, notably in patients with amnesic MCI (Chételat *et al.*, 2003, 2005).

Neuropsychological studies devoted to amnesic syndromes and dementias are of major clinical interest. At a more theoretical level, they are also at the root of the more important concepts in memory research. These neuropsychological studies are also in agreement with studies on pharmacological amnesias which have notably demonstrated dissociations between explicit and implicit memory (Vidailhet et al., 1996).

Over these last twenty years, memory research has been extremely active, both in neuropsychology and cognitive neuroscience. Investigations of permanent amnesic syndromes are at the root of modern theories of memory, but studies today deal with a larger number of pathologies. Their findings, as well as the considerable amount of data coming from neuroimaging studies, have confirmed the usefulness of a plural (or multisystem) view of memory. Numerous concepts corresponding to different systems or subsystems have been proposed. The significance of these concepts has sometimes undergone profound change (e.g. working memory, episodic memory) and it is extremely important to use them in their most precise and up-to-date definition. Frequently - and for a variety of reasons -, research has been conducted into separate memory systems or focused on the relationship between two (rarely more) memory systems or subsystems. However, one major challenge in contemporary memory research is clearly to develop an overarching model that explains how the different memory systems interact, exchange information, and function as a coherent, unified entity in individuals who have normally functioning brains. The review of the literature presented in the next part of this article highlights the relevance of several concepts but strongly underlines the need for a unified account of memory.

Studies of memory have given rise to numerous theories, either modular or parallel distributed models. In this review we deliberately choose to focus on the former which are the most used and the most heuristic in the field of neuropsychology, notably those of Tulving and Baddeley for long term memory and working memory, respectively. Moreover, we also refer to other theories regarding specific concepts and/or systems (Conway, Cermak, Schacter, Anderson…), when necessary.

Short-Term Memory/Working Memory

The classic distinction between short-term and long-term memory, featured in Atkinson and Shiffrin's model (1968), gives a good account of the dissociations described in amnesic syndromes. Thus, the massive impairment of long-term memory in patient HM came to light in various neuropsychological tests, as well as in his behavior in everyday life. On the other hand, this same patient scored normal results in classic tasks of verbal and spatial span assessing short-term memory. For historical accuracy, it is worth noting that the Atkinson and Shiffrin's model included an episodic encoding process. The concept of short-term memory was subsequently replaced by that of multi-component *working memory* (Baddeley & Hitch, 1974; see also Baddeley, 1986). It can be defined as a memory system responsible for the processing and temporary storage of information needed to carry out activities as diverse as understanding, learning and reasoning. This model postulates the existence of two slave systems (the phonological loop and the visuospatial sketchpad), coordinated and supervised by an attentional component, the central executive. The phonological loop is responsible for storing and refreshing verbal information. It is made up of a passive phonological store of limited capacity and a subvocal rehearsal system, which helps to refresh the information and converts a verbalizable stimulus into a phonological code. The visuospatial sketchpad is involved in maintaining spatial and visual information, as well as forming and manipulating mental images. The role of the central executive is to supervise and coordinate the information supplied by the slave systems and overseeing the transfer of information to long-term memory.

Recently, two major advances have contributed to Baddeley's model of working memory. The first of these is a formalization of executive functions which are the core of the central executive, on the basis of structural statistical analyses (Miyake *et al*., 2000). The authors concentrated on three functions which are frequently described in the literature: mental flexibility, updating of information and inhibiting of predominant responses. They showed that while these functions can be clearly distinguished, they also share certain characteristics. Their findings also suggested that the ability to coordinate two activities simultaneously is independent of the other three executive functions they studied.

The second major innovation has come from Baddeley (2000; 2003; Repovs & Baddeley, 2006) himself who postulates the existence of a new temporary back-up store, the *episodic buffer*. The job of the episodic buffer is to act as a temporary storage system capable of integrating information from a variety of sources. It is assumed to be controlled by the central executive, which retrieves this information from the storage systems in the form of conscious awareness, processes this information and, if necessary, manipulates and modifies it. The buffer is *episodic* because it holds episodes whereby information is integrated across space and time. Baddeley and Wilson (2002) have shown that some patients suffering from a severe amnesic syndrome but with no disturbance of executive functions and with preserved intelligence are capable of achieving normal performances on immediate prose recall tasks. Patients with Alzheimer's disease are not.

Baddeley believes that the episodic buffer plays a major role in encoding and retrieving information from episodic memory. This new component of working memory is a *buffer* because it acts as an interface between several systems using different types of encoding. It carries out this interfacing task by using a common multidimensional code. The fact that this buffer is characterized as being episodic immediately emphasizes just how important the phenomenology of recollection and links between consciousness and memory will be in future research. Its assessment in some disease has recently been proven to be useful. Thus, Quinette, Guillery-Girard, Noël, *et al.* (2006) have investigated the nature of the episodic memory impairment in transient global amnesia in distinguishing between the performance of patients with preferential encoding deficits and those of patients with preferential storage disorders. The results showed that while the functions of binding and maintenance of multimodal information (devoted to the episodic buffer) were intact in patients with storage disorders, they were impaired in the case of encoding deficits. These results were easily interpreted in the framework of episodic buffer that represents an interface between working memory and episodic memory.

Long-Term Memory

Episodic memory is defined as the memory of personally-experienced events, situated in the temporal-spatial context of their acquisition. This concept of episodic memory has been undergoing profound and continuous change until recently (Wheeler, Stuss, & Tulving, 1997; Tulving, 2001, 2002). The basic characteristic of episodic memory is that it allows for the conscious recall of a previous experience: the event itself (what), but also where and when it took place. The emphasis is placed not only on the accuracy of the recollection (of the event), but also on subjective experience. Episodic memory is the only form of memory which, at the moment of recall, is turned towards the past. Accordingly, the retrieval of a memory from episodic memory implies “mental time travel” back through one’s past, associated with *autonoetic consciousness*. This concept, which specifically characterizes episodic memory, means that one becomes aware of one’s own identity and existence in subjectively-apprehended time that extends both backward and forward. This definition emphasizes the coming together of three ideas: the self, autonoetic awareness and subjectively-perceived time. The situation of the profoundly amnesic patient KC (see Tulving, 2002, Rosenbaum *et al.*, 2005) gives us some idea of what the absence of episodic memory and autonoetic consciousness means: a feeling of *blankness* and the inability to project oneself into either the past or the future. To sum up, episodic memory encompasses both the accuracy and the subjective experience; these two aspects are remarkably discussed in the theoretical paper of Conway et al. (2004). For these authors, there is "a fundamental tension between adaptive correspondence (experience-near sensory perceptual records of goal activity) and self-coherence (a more abstracted and conceptually-rich long-term store of conceptual and remembered knowledge)".

Semantic memory concerns not only the understanding and use of language (memory of words and concepts), but also the memory of "general facts of the world", including other kinds of stimuli (visual, spatial, etc.). The definition of semantic memory refers to one's *noetic awareness* of the existence of the world and objects, events and other regularities within it, independently of self, autonoetic awareness and subjective time. Semantic memory therefore allows for an introspective attitude towards the world, without the object which gave rise to the thought necessarily being perceptually present, and without the feeling of re-experience which characterizes episodic memory (Tulving, 1972). There is a great deal of neuropsychological data documenting the distinction between episodic and semantic memory, based on diverse methodologies. The preservation of semantic knowledge in amnesic patients displaying massive impairment of episodic memory was first signaled many years ago (Kinsbourne & Wood, 1975) and, more recently, two lines of research have produced some interesting results. The first seeks to highlight dissociations in patients displaying retrograde amnesia by contrasting the normal retrieval of semantic knowledge with the impossibility of recovering episodic memories acquired over the same period (Dalla Barba, Montovan, Ferruzza, & Denes, 1997; Levine *et al.*, 1998; Manning, 2002). The second approach sets out to demonstrate the acquisition of new semantic knowledge by patients incapable of forming new memories. Some amnesic patients can indeed acquire new semantic knowledge, albeit generally at a slower pace than normal subjects (Glisky, Schacter, & Tulving, 1986; Hirst, Phelps, Johnson, & Volpe, 1988). Similarly, in transient global amnesia, Guillery *et al.* (2001) have demonstrated that during the acute phase, patients can acquire new knowledge in semantic memory. In a first step, they were shown sentences that were difficult to understand, together with clues to their meaning. After a more or less lengthy interval (from a few minutes to a few hours), the patients were able to explain these sentences without the help of the clues. This showed that some sort of modification had taken place within semantic memory, even though the patients had no conscious recollection of the initial situation. These findings concur with the observations of developmental amnesia recorded by Vargha-Khadem *et al.* (1997; see also Gadian *et al.*, 2000; Martins *et al.*, 2006), which have triggered fresh debate about the contrast between episodic memory and semantic memory, as well as the role of the hippocampus and related structures in these two memory systems.

Procedural memory allows us gradually to acquire skills through training (i.e. in the course of numerous attempts), store them and reconstruct them without necessarily referring back to previous experiences. It is expressed in the subject's activity and its contents are difficult to verbalize. Procedural memory is an automatic form of memory and cannot easily be accessed by one's consciousness. Even so, *procedural learning* requires the cooperation of several cognitive systems - notably working memory and episodic memory systems - and the subject is therefore partially conscious of the processes involved. Procedural memory *per se* is implicated when subjects are asked to carry out "constant" tasks, characterized by the invariance of the material and instructions, the processing required and the modes of encoding and retrieval, as well as by the involvement of a motor component (Ackerman, 1987). Thanks to the intensive practice of invariant logical conditions, it is claimed that this type of test makes it possible to establish rapid, proceduralized and automatic processes. The constant nature of a task results in a fairly major reduction in interindividual variability in performances during the learning process. Procedural memory is thus gradually brought into play during the automation of a task. This phenomenon has been described within the context of learning theories postulating the existence of different phases (Anderson, 1999). Beaunieux *et al.* (2006) have recently confirmed that three separate learning phases occur during procedural learning (i.e. cognitive, associative and autonomous), in line with the Adaptive Control of Thoughts model proposed by Anderson (1999). Beaunieux and colleagues have also experimentally demonstrated the major involvement of episodic memory and executive functions in the first learning phase. Their cognitive and neuroimaging results show that procedural memory is functionally dependent on high-level cognitive processes in the early stages of encoding, only ceasing to be so when the procedure is fully automated (Hubert et al., in press). The possibility of amnesic patients acquiring new skills has been demonstrated using complex perceptual-verbal-type tests, such as the mirror-reading paradigm, or ones involving complex cognitive strategies, such as the Hanoi Tower (see, for example, Beaunieux *et al.*, 1998, in Korsakoff's syndrome). This memory system would therefore appear to be resistant to numerous pathologies and apparently independent of the structures of the medial temporal lobe. Nevertheless, some patients with episodic memory or working memory deficits may have difficulty acquiring novel semantic and cognitive procedural knowledge (see for example a study of alcoholic patients by Pitel et al., 2007) and procedural memory is affected in various subcortical pathologies, notably fronto-subcortical dementias such as Huntington's disease (Heindel, Salmon, Shults, Walicke, & Butters, 1989). The cerebral substrates of procedural memory comprise various subcortical structures, notably the striatum, as well as the cerebellum.

Implicit memory has given rise to a considerable number of studies in neuropsychology. The terms *explicit* and *implicit* (initially used by E. Claparède to distinguish between two forms of memory processes; see Eustache, Desgranges, & Messerli, 1996) are above all descriptive and, unlike the concepts presented earlier, do not refer to fully-fledged memory systems. This distinction does, however, need to be clarified, as results gathered in this particular field of investigation have allowed us to characterize certain memory systems more accurately. As Schacter (1994) has pointed out, this distinction between different forms of memory has been accompanied by the demonstration of striking dissociations, which would indeed suggest that separate systems are implemented in the implicit and explicit expressions of memory. Moreover, certain findings have led to new memory systems being proposed, such as the *Perceptual Representation System* (PRS; Tulving & Schacter, 1990). The terms *explicit* and *implicit* are also used to describe different memory tasks. Lastly, they can also refer to the psychological experience accompanying information retrieval (Tulving, 2001b). This situation explains why there are so many ongoing terminological and conceptual debates.

According to Schacter, implicit memory is said to be brought into play when previous experiences modify performance on a task which does not require the conscious recollection of these experiences. Explicit memory refers to situations in which a subject consciously recalls information stored in the memory. It can be assessed using the classic memory tests of free recall, cued recall and recognition (although implicit mechanisms are also involved in recognition tasks). Implicit tests of memory rely above all on the search for priming effects. The latter correspond to a phenomenon whereby the one-off presentation of a specific stimulus affects the way that this stimulus or a close or impoverished item is subsequently processed, despite the absence of any conscious retrieval of a previous encounter with this item.

In neuropsychology, the interest in priming effects developed from the work of Warrington and Weiskrantz (1968), who showed that amnesic patients could achieve normal or virtually normal performances on memory tests similar to cued recall but where the reference to the initial presentation of the material was not explicit. However, it was Graf, Squire and Mandler (1984; see also Graf & Schacter, 1985) who clearly underlined the importance of the instructions given to patients during the test phase. Their study focused on cued recall (explicit retrieval) and word-stem completion tasks (implicit retrieval). Whereas the amnesic patients failed to perform as well as the controls on the explicit memory test, both groups achieved comparable results on the implicit task. The interest generated by the implicit memory study gave rise to the creation of a whole host of experimental paradigms, which subsequently generated a great many different classifications based on varied criteria. One of the most frequently-used distinctions is the one between perceptual priming and semantic priming (Tulving & Schacter, 1990). Perceptual priming requires the processing of the overall structure of the stimulus during the test phase and is revealed by clues which provide information about the physical or perceptual properties of the stimulus. Semantic priming involves in-depth processing of the stimulus and the clues supplied during the test phase specify semantic characteristics. This distinction is based on the findings of various studies in experimental psychology, as well as on the observation of demented patients or ones suffering from focal lesions of the brain and characterized by different performance profiles on tasks assessing both types of priming (Keane, Gabrieli, Fennema, Growdon, & Corkin, 1991; Keane, Gabrieli, Mapstone, Johnson, & Corkin, 1995).

In a multisystem concept, such as the one developed by Tulving and Schacter, semantic priming effects are subtended by semantic memory. In a series of articles, these authors have suggested that perceptual priming effects may be subtended by a new memory system, which they refer to as the Perceptual Representation System (see Schacter, 1994). According to them, the PRS is divided into several subsystems which share a number of properties. Probably reliant on cortical mechanisms, they operate at a pre-semantic level (i.e. a level which does not require access to meaning) and are implemented in nonconscious expressions of the memory of past experiences.

Neuropsychology has made a relatively small contribution to the description of the neuroanatomical bases of priming effects, as opposed to other forms or expressions of memory. One reason is that these effects frequently remain intact in cases of brain lesions, including permanent and even transient amnesic syndromes (Kapur, Abbott, Footitt, & Millar, 1996; Eustache *et al.*, 1997). This tends to make them relatively independent of the medial temporal lobe system. Semantic priming effects are frequently disturbed in Alzheimer's disease (Giffard *et al.*, 2001), probably due to dysfunctions in the neocortical regions (Fleischman *et al.*, 2005). Even so, their neural bases are difficult to establish, as quantifying anomalies in semantic priming effects is a complex business, due to the fact that they can be manifested in the form of either hypopriming or hyperpriming (Giffard *et al.*, 2001, 2002). Impairment of perceptual priming effects would appear to be less common, and related studies are certainly less numerous. Anomalies generally follow in the wake of a sensory deficit, and this is why perceptual priming effects are probably subtended by the posterior neocortical regions involved in perceptual mechanisms (Keane *et al.*, 1995; Fleischman *et al.*, 2005). This is supported by activation data collected from healthy subjects in functional imaging of the brain, which also suggest a left lateralization of semantic priming effects and a right lateralization of perceptual priming effects (Lebreton, Desgranges, Landeau, Baron, & Eustache, 2001). Lastly, these studies reveal a strong relationship between the cognitive mechanism of priming effects and their neurophysiological manifestation in the form of a decrease in cerebral blood flow observed during comparisons between priming and reference situations. These results contrast with the findings of studies which have mainly revealed increases in cerebral blood flow in comparisons of explicit memory tasks and reference tasks (Desgranges, Baron, & Eustache, 1998). A fundamental question deals with the physiological meaning of the decrease in cerebral blood flow related to priming effects. Several processes may be at the root of these changes in local synaptic activity. The "repetition suppression" effect, highlighted in physiological studies of monkeys (Desimone, 1996), is characterized by a reduction in the neural response of some neuron ensembles fired of when these items first occurred. However, this striking opposition between increases in explicit memory and decreases in implicit memory that is observed in activation studies needs to be qualified. Thus, some studies involving implicit priming phenomena (see, for example, Henson, Shallice, & Dolan, 2000) have shown increases in cerebral blood flow for primed items, notably during the first occurrence of the priming effect (i.e. when this item has no previous representation in memory).

Memory Concepts and Tasks

According to the concepts presented in this article, with the exception of the terms *explicit memory* and *implicit memory*, which enjoy a special status, the different components described in the previous section correspond to hypothetical systems of memory, and must not be confused with memory tasks, which have been developed within other, frequently older, theoretical frameworks. However, to provide an illustration of the material used in neuropsychological research and establish links between theory and practice, we list the basic definitions of the main concepts and the paradigms currently used by neuropsychologists in Table 1.

[Table 1]

In order to assess multi-component working memory (Baddeley's model), neuropsychologists and experimental psychologists have devised paradigms which make it possible to measure (albeit imperfectly) these different components, namely the phonological store, subvocal rehearsal and visuospatial sketchpad. The proposals put forward by Miyake *et al.* (2000) in particular allow us to rationalize our assessment of the central executive, and it is now possible to use a variety of methodologies to assess the episodic buffer (Prabhakaran, Narayanan, Zaho, & Gabrieli, 2000; Burglen *et al.*, 2004; Quinette, Guillery-Girard, Noël, *et al.*, 2006).

The picture becomes more complicated when it comes to assessing semantic memory, which includes the memory of concepts, knowledge of the world (which varies considerably from one subject to another and is determined by their cultural level) and personal semantics (by definition even more difficult to grasp, as the references are necessarily individual). As for episodic memory, there is an even greater gap between concept and tasks. Neuropsychological tests assess episodic memory extremely imperfectly (or partially). It is a serious problem, as this system is impaired in many pathological situations (especially neurodegenerative diseases such as Alzheimer's), as well as in the normal aging process. It is important to distinguish between episodic memory tasks (the classic tests of free recall, cued recall and recognition on which neuropsychological tests are based) and the concept of episodic memory, which emphasizes the subjectivity and phenomenology of memory. Even so, certain tasks do enable us to gain a better idea of the specificity of episodic memory, notably certain assessments of autobiographical memory (Piolino *et al.*, 2003; 2006).

Recognition tests deserve particular attention, because their ease of use makes them extremely popular, though they do pose specific problems. At first glance, these recognition tests ("Indicate whether or not you have already been shown this item") would appear to assess episodic memory. However, many studies have suggested that this interpretation is only partly correct, and that the tests may actually span two separate processes or types of memory: recollection and familiarity (see Yonelinas, 2002, for a review). Studies using the

Remember – Know (R-K) paradigm are especially revealing (Tulving, 1985, Gardiner, 1988, 2001). In this type of paradigm, subjects taking part in the recognition test must answer a supplementary question when they think that they have already been shown the item. They must decide whether they *remember* the event corresponding to the presentation of the item during the study phase or whether they *know* that this item was on the initial list because of a simple feeling of familiarity. More precisely, during the recognition task, the subject has to give a "Remember" response if recognition is accompanied by the retrieval of the context in the form of a re-experiencing of information from the learning context (i.e. thoughts, feelings or perceptions) and a "Know" response if recognition is achieved without any such access. In addition, "Chance" or "Guess" responses give subjects the possibility of signaling when their recognition judgment of an item is a matter of chance ("I guess that this item may be a target item but I do not remember or even know that I saw either one or the other of these two items"). The R-K paradigm is intended to gauge states of consciousness associated with memory retrieval (Tulving, 2001b). As such, in the context of multisystem theories, the R-K paradigm constitutes a sound approach to autonoetic consciousness and noetic consciousness, associated with episodic memory and semantic memory respectively. Although methodological problems do not fall within the ambit of this article, this dichotomic vision does need to be qualified somewhat. First of all, the use of R responses (corresponding to mechanisms of conscious retrieval) indubitably represents an interesting contribution to the assessment of episodic memory, providing that the material is suitable for this form of investigation (i.e. genuinely allowing the scene to be relived). Secondly, K-type responses (corresponding to a feeling of familiarity) probably cover very different realities, ranging from noetic consciousness, which describes semantic memory, to purely perceptual familiarity (Aggleton & Pearce, 2001; Morris, 2001). Otherwise, qualitative characteristics of each memory can also be assessed by asking the subjects to report their *self-perspective* during retrieval (for details see Piolino et al., 2006, and Piolino et al., 2007, for an application in frontotemporal dementia). The estimation of self-perspective accompanying mental imagery related to each memory can be made thanks to the field/observer paradigm (Nigro and Neisser, 1983). The subjects are required to give either *observer* response if they saw themselves in the scene as a spectator or a *field* response if they saw the scene through their own eyes, as if they were reliving the event from something like the original perspective as an actor would.

Methodologies for assessing procedural memory are fairly standardized: subjects are asked to make several attempts at performing an unfamiliar task, and a learning curve is established by measuring their performances in terms of precision and/or duration. The performances of amnesic patients are often poorer than those of controls (learning takes longer, for example) and are sometimes considerably disturbed. These results are generally ascribed to the impairment of episodic memory and working memory, which hinders the activation of the procedural learning process. The problems associated with the assessment of procedural memory are therefore very different from those encountered when assessing episodic memory, for instance. The difficulty here lies in trying to distinguish between the processes involved in procedural learning and procedural memory *per se*. Accordingly, rather than measuring procedural memory, current assessments actually measure procedural learning in its initial phases, when procedural memory is virtually absent. However, if the number of trials is sufficient (at least 40 trials of the Tower of Hanoi, for example), it is possible to make a valuable assessment of procedural memory (Beaunieux *et al*., 2006; see also Hubert *et al*., 2007 for a validation using functional cerebral imaging).

The situation is different yet again when it comes to measuring priming effects. This involves methodologies developed in experimental psychology and psycholinguistics which have only recently been applied to neuropsychology. They continue to be used mainly for research purposes (with the exception of word-stem completion paradigms, which are sometimes used by clinicians) and, for this reason, the distance between concepts and assessment is not as great.

Multisystem Concepts of Memory

As Baddeley recently stressed (2000), the different theoretical models, emanating from a variety of sources, apply either to precise phenomena or to far more general frameworks. In the latter case, they seek to give account of a large body of familiar data, all the while opening up avenues for future research, deliberately relegating more detailed specifications to the background. This is a useful approach at the present time, given the welter of empirical results amassed over the last twenty years or so in memory-based research.

It was in the early 'eighties that Tulving first proposed the existence of a "monohierarchical arrangement", in which episodic memory constituted a specialized subsystem of semantic memory which, in turn, was a specialized subsystem of procedural memory. This organization excluded the possibility of double dissociations, as the high-level systems in the hierarchy were placed in a relation of dependency with the lower-level systems. Tulving supplied ontogenetic and phylogenetic arguments to support this "Russian doll" organization of the various systems. In the " monohierarchical interlocking" model, Tulving (1985) matches three forms of consciousness (i.e. autonoetic, noetic and anoetic) to the three systems of memory (episodic, semantic and procedural, respectively).

The significant development in the early 'nineties was the addition of two new memory systems: the PRS and working memory. These five memory systems constitute the framework within which the author proposed his *SPI* (serial-parallel-independent) model in 1995. This model therefore brings together the two major concepts governing the structural and functional description of memory: systems and processes. The *SPI* model is also an attempt to overcome the inflexibility of previous monohierarchical concepts, notably the impossibility of highlighting double neuropsychological dissociations (Figure 1). According to this model, there is a serial dimension to encoding (encoding in one system depends on the quality of the encoding in the lower system), storage occurs in parallel in the different systems, and the retrieval of information stored in one system takes place independently of retrieval from other systems. This model therefore predicts that the encoding of an item of information at a "lower" level (e.g. semantic memory) can take place even if encoding at a higher level (episodic memory) is impaired, but not the other way round (which remains a considerable constraint). When it comes to retrieval, however, there are far fewer constraints. For example, the *SPI* model does not exclude the possibility that retrieval of semantic information may be impaired while retrieval from episodic memory remains intact. It thus allows us to give account (at least partly) of certain double dissociations encountered in dementias, notably impaired semantic memory at the early stage of semantic dementia.

(Figure 1 about here)

In the *SPI* model, this organization holds good for the four representational systems, but not for the procedural memory action system. Relations between procedural memory and the other systems are not specified, and this constitutes one of the model's limitations. In subsequent publications (see, in particular, Tulving, 2001a), the emphasis has been placed on relations between the PRS, semantic memory and episodic memory. Nor are links with working memory specified, and this represents a further limitation, especially given the significant developments that have taken place in this field, notably Baddeley's proposition (2000) of the existence of an episodic buffer at the interface between "short-term" and "long-term" structures.

Tulving (2001a) has defended the configuration of the *SPI* model, restricted to the PRS, semantic memory and episodic memory systems, in a debate with Hodges and his colleagues (see Hodges & Graham, 2001, for a review). These authors adopt a divergent opinion about the need for information to be transmitted from the PRS via semantic memory in order to reach episodic memory. In a series of publications, Hodges and his colleagues have shown that patients in the early stages of semantic dementia achieve normal performances on various recognition tasks using non-verbal material (drawings, faces, etc.). Providing the stimuli do not undergo any alterations between the study and test phases, the performances of these patients are perfect, whether the items are known (the patients can name them) or unknown. As soon as these stimuli are modified, however (e.g. photos of objects taken from different angles), successful recognition becomes dependent upon the semantic status of the stimulus: a high level of recognition for known items, but impaired recognition for unknown stimuli. For the authors, this series of experiments suggests that there are multiple inputs into episodic memory and that perceptual information about the items being studied can – generally in conjunction with the semantic system, but also in the absence of all meaning – generate fresh learning. This type of acquisition, which has no recourse to the semantic system, only works for non-verbal material, not for words (Graham, Patterson, Powis, Drake, & Hodges, 2002). In their opinion, these findings contradict Tulving's *SPI* model (1995), according to which acquisition in episodic memory necessarily relies on the semantic system, and they have put forward an alternative hypothesis, the Multiple Input Model (MIM). According to this model, information from the perceptual system can directly enter episodic memory, thereby explaining the normal recognition performances in patients suffering from semantic dementia, whereas in normal subjects, recognition memory relies on multiple inputs from both the perceptual and semantic systems.

Tulving (2001a) has given a clear and vigorous response to the propositions made by Hodges' team: there is no possibility in *SPI* for the direct encoding of perceptual information in episodic memory. Hodges and his colleagues (Simons *et al.*, 2002) sought to respond to this criticism by asking patients suffering from semantic dementia to perform tests bringing recollection mechanisms into play, within the framework of a thorough item-by-item analysis (matching the performances of the same patients with the same items and different tasks). Most of the patients successfully carried out these tasks and, most important of all, the status of their semantic knowledge did not allow the researchers to predict their results in the two memory tests. These findings are of interest because they show that patients suffering from semantic dementia can acquire elements of an episodic memory (the source of the event, the association of two stimuli), but they do not go any way towards solving the problem of how a complete episodic memory can be formed without any semantic mediation. However, according to Tulving, Yes-No recognition tasks can be regarded as "episodic memory tasks", yet they do not correspond to its updated definition and successful performances could be linked to the involvement of perceptual memory without any semantic or episodic mediation. Direct links between PRS and episodic memory have also been suggested by the recent study of Gagnepain et al. (2007) that sought to assess the impact of perceptual priming on the creation of new episodic memories. Results showed that the more the perceptual priming was high, the more the encoding of new episodic memories was enhanced. This suggests that a significant relation between perceptual priming and episodic memory performances rests on a mechanism allowing to the new episodic memories creation to be directly enhanced by perceptual priming at encoding. Thus, this study brings an interesting gap between the automatic unconscious process that is perceptual priming and the higher degree of human consciousness that is episodic memory. Last but not least, it could be also interesting to consider perceptual representations stored into perceptual memory, which are different for everyone, as belonging to a "perceptual self". From this perspective, when episodic memories are not extensively associated to autobiographical knowledge (Conway, 2001; Conway & Pleydell-Pearce, 2000), integration of highly perceptually primed representations into episodic memories would be a key mechanism to mentally relive this event as being self experimented. If these findings are confirmed by other studies, and particularly in patients with semantic dementia, the direct link between PRS and episodic memory should be taken into account and better understood.

Tulving lists four other characteristics of the *SPI* model. First of all, memory can function perfectly well at lower levels, independently of high-level systems. Some learning therefore takes place at a strictly perceptual level, without any intervention from either semantic memory or episodic memory. This, for instance, is the case in animals (Aggleton & Pearce, 2001) and young children (Rovee-Collier & Hayne, 2000), as well as in various object recognition tasks such as delayed non-matching to sample. For Tulving – and this is a fundamental characteristic of his model – a considerable volume of information (general knowledge) can be acquired without the intervention of episodic memory. This type of acquisition has been shown to take place in normal children (see Wheeler *et al.*, 1997) and, in the case of certain amnesic syndromes, both adults and children (see above). This is the greatest argument against the model put forward by Squire and his colleagues (Cohen & Squire, 1980; Bayley & Squire, 2003). Secondly, the *SPI* model allows for and even predicts double dissociations between episodic and semantic memory in the context of retrograde amnesias. This aspect also distinguishes it from Squire's model, which predicts the combined impairment of fact memory (semantic memory) and event memory (episodic memory), which go to make up declarative memory. Thirdly, *SPI* does not allow for double dissociations between episodic and semantic memory in the context of anterograde amnesias. When a patient presents with an anterograde amnesia, this may be either an episodic and semantic disorder (the standard form of anterograde amnesia), or a strictly episodic one. In other words, a purely semantic anterograde amnesia is inconceivable, according to the *SPI* model. Lastly, the early version of the model (Tulving, 1995) was a psychological theory, whereas it is now a neuroanatomical model. While the implication of the frontal cortex had already been highlighted (Tulving, Kapur, Craik, Moscovitch, & Houle, 1994; Wheeler *et al.*, 1997), the emphasis is now placed on the hierarchical organization of the medial temporal lobe put forward by Mishkin, Vargha-Khadem and Gadian (1998): the hippocampus acts at the highest level of the hierarchy and is associated with episodic memory, whereas the adjacent cortical regions intervene at lower levels and are associated with semantic memory (see also Tulving & Markowitsh, 1998; Aggleton & Brown, 1999).

MNESIS: a Provisional Synthesis

(Fig 2 about here)

Figure 2 represents a proposed synthesis of what appear to be the most relevant theories in the neuropsychology of memory at the present time. MNESIS (short for Memory NEoStructural Inter-Systemic model) integrates the soundest elements of the multisystem concepts, while specifying the relations between the various systems, based on data from existing literature. Although MNESIS is, in essence, temporary, pending advances in the fields of neuropsychology, cognitive neuroscience and neuroimaging, we think it could prove useful to researchers and clinicians at the present time, notably in formulating hypotheses about the relationships between memory systems from theoretical as well as clinical perspectives.

Long-term cognitive representation systems: a monohierarchical arrangement

To the left of the diagram, three systems (perceptual memory, semantic memory, episodic memory) are shown in the hierarchy proposed by Tulving (2001a). The definitions of episodic memory and semantic memory reflect the most recent propositions by this author and his colleagues, which are set out in this article. However, the term "perceptual memory" replaces the Perceptual Representation System (PRS) which, according to Schacter's definition (1994), only covers nonconscious expressions of memory and may therefore introduce a degree of ambiguity into a number of experimental situations bringing memory mechanisms into play on a perceptual basis and in a conscious fashion. The concept of "perceptual memory" is broader than that of the PRS, as it includes both conscious and nonconscious operations. The extension of the initial concept makes it possible to provide potential explanations for the unexpected preservation of memory performances in semantic dementia (see above). These abilities could rely on this perceptual memory system, rather than episodic memory.

To the left of these three representational systems are two arrows, which should be regarded as retroactions. One (going from episodic memory to semantic memory) designates the process of memory semanticization (Cermak, 1984), which in no way contradicts Tulving's sound hypothesis that information is encoded in semantic memory before being encoded in episodic memory. This retroaction indicates that memories tend to become semanticized over time, though not all memories necessarily become semanticized, and true episodic memories do exist, even for the far-distant past (Piolino *et al.*, 2006). The theory of the "semanticization" of episodic memories was initially proposed by Cermak (1984) to explain the episodic-semantic distinction in amnesia. Cermak expounded the idea that episodic memory and semantic memory form a continuum in order to explain Ribot's temporal gradient, whereby the most remote periods are the best preserved in retrograde amnesia. According to him, Ribot's gradient is due to the greater vulnerability of episodic memory to amnesia and "even those distant episodes that do appear vivid may actually be more familial folklore than truly retained episodes' (Cermak, 1984, p. 59). This theory has recently been illustrated by findings obtained in Alzheimer's disease in a Positron Emission Tomography (PET) study of autobiographical amnesia (Eustache *et al*., 2004). Using a specially-designed questionnaire covering three broad time periods (the previous five years, middle age, teenage years and childhood), we showed that Alzheimer's patients performed more poorly than a control group for all three time periods and that they displayed Ribot's gradient. A qualitative analysis showed that remote memories in the patients concerned generic (i.e. semantic) events rather than specific (i.e. episodic) ones. Moreover, we applied a correlative approach to temporally-graded memory scores and resting cerebral utilization measured by PET in these patients. Broadly speaking, our results showed that the retrieval of recent memories was linked to cerebral structures involved in episodic memory, such as the hippocampus and the right prefrontal cortex. Conversely, the retrieval of remote memories was linked to cerebral structures involved in semantic memory, notably in the left middle frontal gyrus. Our findings highlight a shift in the laterality of correlations within the prefrontal cortex over time, from the right to the left hemisphere. This may reveal a transition from episodic to semantic retrieval, consistent with both the theory of semanticization and the Hemispheric Encoding Retrieval Asymmetry (HERA) model (Tulving *et al*., 1994), based on activation studies in healthy subjects. Indeed, according to the HERA model, the right and left prefrontal cortices are preferentially involved in the retrieval of episodic memories and semantic information respectively.

While these findings illustrate the transition from episodic to semantic memory over time, this change is not systematic, as some early episodic memories may persist in normal elderly subjects (Piolino *et al*., 2006) and even in Alzheimer's disease patients (Piolino *et al*., 2003). Interestingly, our findings may also be considered in conjunction with the view that episodic memory is essential for the retrieval of recent memories, whereas semantic memory is essential for the retrieval of remote ones. Indeed, in numerous situations, semantic memory is essential for recollecting remote episodic memories. According to the constructive model of autobiographical memory proposed by Conway (2001; see also Conway & Pleydell-Pearce, 2000; Conway et al., 2004), a complex cyclical retrieval process which depends on the frontal lobe, especially the left side, allows us to access sensory/perceptual event-specific knowledge through the personal knowledge base (personal semantic memory). Autobiographical memory therefore reflects the integration of episodic information with knowledge structures in long-term memory. Thus, our results reflect the semantic establishment over time of a retrieval route to episodic knowledge structures in other areas of the brain.

The second arrow (from episodic memory to perceptual memory) refers to the transfer of perceptual memory traces during the phenomenon of re-living experiences, which happens both consciously and unconsciously (including during dreams). This process can be followed up by re-encoding in episodic memory and thus contributes to the process of memory consolidation.

Indeed, any overall model of memory must feature mechanisms of consolidation, slow process whereby a still labile memory trace is converted into a more permanent or enhanced form, notably by establishing connections between the medial temporal lobes and neocortical areas. These consolidation mechanisms are still largely misunderstood and the concept proper refers to very different temporal dimensions (short term and long term consolidation) and applies to several memory systems. Thus demonstrative results have been recently obtained in the field of sleep research, particularly in sleep deprivation and functional neuroimaging studies.

In a review paper (Rauchs, Desgranges, Foret, & Eustache, 2005), we summarized the key findings for the role of sleep in the memory consolidation of both animals and humans, and tried to establish links between sleep stages (notably Non-Rapid Eye Movement (NREM) and Rapid Eye Movement (REM) sleep) and the various long-term memory systems. Thus, several lines of evidence support the hypothesis that sleep is involved in the off-line reprocessing of recently-acquired memories. All the various studies emphasize the fact that the long-term memory systems benefit either from Non-Rapid Eye Movement or Rapid Eye Movement sleep or from both sleep stages. Broadly speaking, the classification of memory systems proposed by Tulving, and largely adopted in MNESIS for the long-term cognitive representation systems, appears more relevant than the simple declarative/non-declarative dichotomy when it comes to understanding the role of sleep in memory. Even if recourse to the concepts analyzed in this article (PRS, semantic memory, episodic memory) does not clarify all the relationships between the different sleep stages and memory systems, it does allow us to resolve several contradictions, notably the fact that episodic and semantic memory (the two memory systems encompassed in declarative memory, the concept frequently used in sleep studies) appear to rely on different sleep stages. Our review shows that both perceptual priming and semantic memory appear to rely on REM sleep. Regarding episodic memory, the numerous studies assessing this memory system have provided mixed results: beneficial effect of NREM sleep, REM sleep or both. The use of tasks that do not truly fit the definition of episodic memory and the fact that different aspects of memory (temporal/spatial) rely on different sleep stages may account for these inconsistencies.

Overall, the three long term representation systems and the two retroactions, which correspond to large-scale phenomena, help to underline the dynamic and reconstructive nature of memory (Conway & Pleydell-Pearce, 2000), and their potential corollary, false memories (Schacter, 1996).

Working Memory and Procedural Memory: Interactive Systems outside the Hierarchy

Working memory remains at the center of Figure 2, with the components of Baddeley's "classic" model (central executive, phonological loop, visuospatial sketchpad) on one side and the episodic buffer on the other. The latter occupies a strategic position within the overall memory systems. Because of its newness, its relations with the other systems have yet to be properly specified, although we already know that it enjoys a special relationship with the central executive and episodic memory. The interactions between the episodic buffer and the central executive and episodic memory will form a key research topic over the coming years (Baddeley, 2003). The interest of the concept of episodic buffer, at the boundary between short term and long term memory systems, has already been demonstrated in various pathologies, notably transient global amnesia (Quinette et al., 2006) and schizophrenia (Burglen et al., 2004). Future works are needed to better understand the relationships between executive functions and the central executive of working memory.

Procedural memory is shown on the right-hand side of the model, with the support of perceptual-motor skills at the lower level and that of perceptual-verbal and cognitive skills at the higher one (no strictly separate procedural systems are postulated). Given the mass of data that is now available, especially concerning the strength of dissociations with declarative memory systems, the time has come to postulate the existence of a procedural memory system in humans, similar to that which has been found in animals, although the interactions between this action system and the representational systems first need to be defined more clearly. This explains the various arrows linking it to the other memory systems. The strongest links with perceptual memory are for perceptual-motor procedural memory, while the strongest ones with episodic memory are for cognitive procedural memory. In every case, interactions with the representational systems (including working memory) are particularly important during the phase of procedural learning, these links subsequently weakening during the process of automation (Beaunieux *et al.*, 2006). In the same vein, recent imaging studies have shown an involvement of a frontoparietal network in the time course of learning of a cognitive procedure, this involvement being particularly massive at the beginning of the learning, due to the intervention of several cognitive processes, notably working and episodic memory (Anderson, Albert, & Finchman, 2005; Hubert *et al.*, 2007).

Regarding the different components of procedural memory, consolidation processes also need to be explored. As for the long-term representation systems, several lines of evidence support the hypothesis that sleep is involved in these phenomena. Hence, it appears that, within procedural memory, consolidation of perceptual-motor skills relies mainly on NREM sleep, with some evidence also suggesting the possible involvement of REM sleep. REM sleep may also have a beneficial effect on the consolidation of cognitive skills, whereas the consolidation of perceptual skills appears to rely more consistently on a combination of both NREM and REM sleep (Rauchs *et al.*, 2005).

Numerous Questions Surrounding MNESIS and only some Temporary Responses

The prime objective of MNESIS is to select concepts used in the neuropsychology of human memory, specify how they fit together and define the links between them more clearly. These concepts correspond to systems or subsystems of memory (e.g. working memory, episodic memory, etc.) that meet with general consensus (albeit rather relative for some of them, such the episodic buffer, the “new kid on the block”). These concepts must not be confused with terms describing materials, tasks or procedures and can in no way be compared to memory tasks. That said, although no test can specifically measure a given memory system, for experimental and clinical purposes, it is vital to develop tools that match the concepts featured in MNESIS as closely as possible (see Table 1).

A number of familiar concepts have been excluded from the architecture of MNESIS, such as short-term memory, which is replaced by the concept of working memory. This is because these two terms are sometimes regarded as synonymous, sometimes as different, and this can lead to misunderstandings. Other terms may not be featured in the architecture but are used for descriptive purposes (notably in this review article), for characterizing processes, tests, etc. This category includes concepts such as "implicit" and "explicit", which may not correspond to actual memory systems but can still serve a useful purpose (e.g. "declarative memory" is a helpful term in situations where episodic and semantic memory need to be grouped together). Other terms, mostly used to describe study material (e.g. verbal memory, visual memory, spatial memory, etc.) have not been given the status of memory system either, even though their theoretical importance may transcend the mere description of material (see for example spatial memory, Moscovitch *et al.*, 2005). Lastly, despite the fact that it has been the subject of major theoretical developments, the term "autobiographical memory" also belongs to this category, as it refers to material of considerable complexity and numerous memory concepts are needed to give account of it at a theoretical level.

Some questions are not specific to MNESIS and also apply to the models from which it is derived, such as the relations between episodic memory and semantic memory, or the organization of working memory. However, it is important to stress that MNESIS does not strictly espouse all the positions held by the authors or schools responsible for the main models on which MNESIS is based (e.g. SPI and Baddeley's conceptions of working memory).

For example, MNESIS adopts the monohierarchical organization of memory systems of long-term representation. That said, it is vital to take account of current "hot topics", particularly the relations between episodic and semantic memory. Patients suffering from semantic dementia who achieve normal performances on certain episodic memory tasks featuring semantically-degraded material would appear to contradict the strict hierarchical organization of these two systems. It is these findings that have led Hodges and his colleagues to put forward an alternative model, whereby information can pass directly from perceptual memory to episodic memory. Even if we find it difficult to conceive of a fully-fledged memory being formed without the involvement of semantic memory, and even if it is tempting to criticize the nature of the tasks used to assess episodic memory in these studies (and therefore to reject the Multiple Input Model), episodic-semantic links deserve to be reconsidered. Other observations carried out among patients suffering from semantic dementia show the same tendency, with the preservation and even more relearning of certain semantic knowledge – knowledge based on the patients' own experiences (Snowden & Neary, 2002). Accordingly, the imprint left by the spatiotemporal context on certain concepts could turn them into specific concepts unique to one individual, a sort of "mixed" representation. Above and beyond the relearning of concepts, there remains the question of whether it is possible to form genuine memories in the case of impaired semantic memory. At this level, the influence of self could prove decisive, just as personal relevance plays a crucial role in the retention of autobiographical memories (Joubert, Mauries, Barbeau, Ceccaldi, & Poncet, 2004).

In short, the opposition between semantic and episodic memory is crucial, but the possibilities of interaction between the two have certainly been underestimated. The retroactions suggested by MNESIS are vital if we are to give account of the dynamic relations between concepts, particularly between episodic and semantic memory. These relations are probably linked to the importance to the self of the information being processed. Moreover, the hierarchical organization suggests that a positive connotation is attached to episodic memory, which is widely regarded as the most sophisticated form of memory, specific to humankind and indissociable from autonoetic consciousness and self-awareness. Our identity may be built on unique events which give rise to episodic traces, but it is also and possibly above all built on the repetition of events that have lost their context (partially at least) - in other words, semanticized representations (see for example Conway *et al.*, 2004).

MNESIS provides a theoretical framework that can help to resolve an extremely wide range of questions: How do these interactive systems develop in children? How do they change during the aging process? How are they affected by diseases of the brain? Although the SPI model can give account of much of the data, it would appear to be insufficient to answer all these questions. In particular, unlike the SPI, MNESIS gives procedural memory a place in its own right, and its relations with the other systems are highlighted and presented from a dynamic perspective. For instance, MNESIS gives account of the difficulty of acquiring complex procedures in the event of impaired working memory and episodic memory. Similarly, the acquisition of perceptual-motor procedures is shown as relying on working memory and perceptual memory. Furthermore, the difficulties in acquiring procedures observed in subcortical pathologies have sometimes been interpreted as an argument in favor of the independence of procedural memory from other memory systems. In actual fact, these pathologies are accompanied by working memory disturbances which may hamper the acquisition of procedures. In this case, the question of the selective impairment of procedural memory can only be answered by administering a test in which all other cognitive disorders can be overcome (e.g. by providing help in compensating for them).

Lastly, MNESIS is a theoretical model arising mainly from clinical neuropsychology. As such, it is eminently suitable for guiding clinicians in their assessment or treatment of patients. To return to the example of procedural memory, the MNESIS model indicates that its assessment needs to take into account other memory capacities and any rehabilitation program must seek to compensate for any deficits of episodic or working memory in order to facilitate the acquisition of procedures, as is the case of errorless learning (Wilson, Baddeley, Evans, & Shield, 1994).

MNESIS: an Open Model for the Future

MNESIS thus comprises five memory systems, like Tulving's *SPI* model (1995), from which it is derived. It retains the original organization of the three systems of long-term representation, but adds retroactions to them (i.e. semanticization, consolidation), in order to give account of the dynamic and reconstructive nature of human memory. It also integrates new interactions between these three systems and working memory on the one hand, taking on board the recent developments presented by Baddeley, and procedural memory on the other hand, referring to learning theories developed in cognitive psychology and still relatively underused in neuropsychology. This model places memory at the heart of the psyche. It can be likened to the notion of self-awareness, which generates a subjective impression of the self in time, linked to feelings of wholeness, continuity and inner coherence. Links with the emotions are not shown in this model, as they intervene in all the different systems, as well as during their various interactions, though microsystems need to be devised in order to specify the relations between memory and emotions at different levels of analysis. MNESIS is an overall model of human memory which can be used for either teaching or research purposes, especially in neuropsychology and neuroimaging, and during exchanges with experts in the cognitive psychology of both humans and animals. It can serve as a basis for discussing the different profiles of memory disorders and different cerebral locations, as well as a frame of reference in multidisciplinary discussions aimed at harmonizing memory systems and processes.

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Captions

Figure 1: Tulving's *SPI* (serial-parallel-independent) model (1995). This model comprises five systems: an action system (procedural memory) and four systems of representation. The latter's organization depends on the processes: encoding is serial, from the PRS upwards, storage takes place in parallel in the different systems and information retrieval takes place independently of retrieval from the other systems.

Figure 2: MNESIS (Memory NEoStructural Inter-Systemic model). This model, which comprises five memory systems, integrating the concepts developed by Tulving (1995, 2001) and Baddeley (2000), highlights relations between different systems in order to give account of the dynamic and reconstructive nature of human memory, with reference to the theories notably put forward by Conway (2001) and Schacter (1996).
Three long term representation systems (perceptual memory, semantic memory, episodic memory) are embedded in a hierarchical way, as in the SPI model elaborated by Tulving. However, MNESIS contains specific particularities. The term "perceptual memory" replaces the Perceptual Representation System, and thus includes both conscious and nonconscious operations. Furthermore, contrary to SPI, direct links between perceptual memory and episodic memory are possible, even if further studies are needed to clarify up to which point. In the same vein, MNESIS allows to take account of current "hot topics", such as the concept of personal relevance to better characterize the interrelations between episodic and semantic memory. In MNESIS, the three long term representation systems are also connected by two (retroaction) arrows. The first one, going from episodic memory to semantic memory, designates the fundamental process of memory semanticization. The second arrow, going from episodic memory to perceptual memory, refers to the transfer of perceptual traces during the phenomenon of re-living experiences, that can be followed up by re-encoding in episodic memory and thus contributes to one form of memory consolidation. Overall, the organisation of the three long term representation systems together with the two interactions underlines the dynamic and reconstructive nature of memory. Working memory occupies a strategic position within the overall memory systems. The interactions between the episodic buffer and the central executive and episodic memory will form a key research topic over the coming years. Procedural memory is shown on the right-hand side of the model. MNESIS specifies the interactions (formulated by arrows) with the representation systems (including working

memory) during the phase of procedural learning, these links subsequently weakening during the process of automation.

Table 1: Basic concepts used in memory models: definitions (see text for details) and examples of tasks used in clinical neuropsychology

	Definitions	Main tasks
Working memory		
Phonological loop	Responsible for storing and refreshing verbal information.	Forward verbal span
Visuospatial sketchpad	Involved in maintaining spatial and visual information	Forward visual span
Episodic buffer	Temporary storage system capable of integrating information from a variety of sources	Immediate prose recall Integration task (Prabhakaran *et al*., 2000; Quinette, Guillery-Girard, Noël, et al., 2006)
Central executive	Supervises and coordinates the slave systems (includes executive functions)	Backward spans; dual tasks; Trail-making test (mental flexibility); N-back test (updating); Stroop (inhibition) (Miyake *et al*., 2000)
Long-term memory		
Episodic memory*	Memory of personally experienced events, situated in the temporal-spatial context of their acquisition Associated with *autonoetic consciousness*	Wechsler memory scale (Wechsler, 1997) California Verbal Learning Test (Delis, Kramer, Kaplan, & Ober, 1987) Selective reminding test (Grober & Buschke, 1987) Rey figure (Rey, 1959) Doors & People (Baddeley, Emslie, & Nimmo-Smith, 1994) Remember/Know paradigm (Tulving, 1985; Gardiner, 1988) : R responses
Semantic memory	Memory of general facts of the world Associated with *noetic consciousness*	Explicit tasks: Pyramids and Palm Trees test (Howard & Patterson 1992) Naming tasks; Verbal fluency tasks Remember/Know paradigm (Tulving, 1985; Gardiner, 1988): K responses Implicit task: category exemplar test
Perceptual representation system	Subtends perceptual priming effect	Perceptual identification tasks (Lebreton et al., 2001)
Procedural memory	Allows skills to be acquired through training	Rotor test (perceptual-motor); Mirror reading (perceptual-verbal); Tower tasks (cognitive) (Beaunieux et al., 2006)

* Most of episodic memory tasks assess the accuracy, while the remember/known paradigm allows to evaluate the subjective experience.