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NEUROCOGNITIVE FOUNDATIONS OF HUMAN MEMORY

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Memory research has traditionally been segregated into (a) research on the cognitive organization of memory and (b) research on the brain basis of memory. As a result of this segregation, cognitive theories of memory have generally evolved in isolation from neuroscientific theories of memory, and vice versa. Moreover, cognitive theorists have regularly found that neural evidence is not relevant to their theorizing. Neuroscientists, on the other hand, are centrally concerned with understanding how the brain works, and their work has usually not made contact with efforts to understand how the mind works.

Nonetheless, new connections between cognitive science and brain science are evident in a wide variety of domains. Advances in measuring human brain function, for example, have increased the likelihood that relevant information about how the brain works can be used to discover how the mind works. In memory research, there is now a growing trend to use neural information to inform theories of memory (Gabrieli, 1998; Schacter, Norman, & Koutstaal, 1998). This approach requires an appreciation of both the brain substrates of memory and the cognitive organization of memory, and seeks to develop bridges between theories couched at these different levels.

Here, I will make the case that measures of the electrical activity of the human brain, in particular, can be used as powerful tools for studying human memory. Associations between memory functions and electrophysiological

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measures will be interpreted not merely within the context of studies of brain potentials, but within a broader theoretical perspective that addresses both the cognitive structure (as in a characterization of relevant cognitive processes and their interrelationships) and the neural implementation of memory functions. Therefore, I will begin with a discussion of the general problem of bridging neural and cognitive levels. I will then outline a framework for thinking about the neurocognitive foundations of certain types of memory. Finally, I will explore the prospects for future advances based on measuring the electrical activity of the human brain.

I. What Evidence from Neuroscience Is Relevant for Understanding Cognition?

Contact between cognitive and neuroscientific approaches is important if one is concerned with the goal of improving our understanding of the cognitive functions of the human brain. To achieve this goal, it would be helpful to determine which facts about the brain might be relevant. It is disappointing, then, that there is no widely agreed upon set of criteria for making this determination.

In addressing this issue, it is instructive to first consider an alternative goal. At one extreme, some prefer to assume that no brain facts are relevant. Indeed, a great many cognitive scientists have developed functional models of cognition that make no reference to the brain. Three brief arguments against this approach are as follows. First, unless one holds the view that the mind emanates from something other than the brain, one must accept the view that cognitive functions are inherently functions of the brain. It follows that ignoring the neurophysiological substrates of cognitive functions is detrimental to gaining a comprehensive understanding of cognition. Second, scientific theories should be tested using the most extensive basis of empirical evidence available. Indeed, cognition is not measured directly—it is fundamentally an inference based on behavioral observations. Cognitive theories can thus be improved by including a basis of both behavioral and neural observations. Third, whereas behavioral evidence is obtained only after complex interactions among multiple cognitive processes lead to a response, neural evidence is not subject to this limitation. Online measures of brain activity offer the remarkable possibility of tapping into relevant processes as they occur, perhaps facilitating the individuation of component cognitive processes. In short, the understanding that cognition arises from the brain leads naturally to the position that models of cognition should be based on relevant evidence of both behavioral and neural varieties.

Another extreme position that should also be considered is that *all* neuroscientific information is relevant to cognitive theory. This position is based on the premise that we do not know in advance how cognitive functions are related to the neurophysiology of the brain. Therefore, we cannot know in advance precisely which evidence will or will not ultimately be relevant. Indeed, neuroscientific facts at the level of detail of the molecular structure and genetic coding for various neuroreceptors may benefit a future understanding of some aspects of cognition. In the absence of a fully developed theory of cognition, perhaps all such neural information should be made available to cognitive scientists. Nevertheless, this view is problematic because it conflates two concerns: how future conceptions of the mind will unfold and how the development of cognitive theories can proceed at present.

How can we evaluate the relevance of any given neural evidence for developing our *current* understanding of cognition? Clearly, approaching this question with respect to a specific case, as attempted below, is more feasible than providing a universal answer. How the evaluation process will play out depends on the extent to which a hypothetical description of the neural implementation of the cognitive function in question can already be given. If little is known about the neural implementation of a cognitive function, it is difficult to know where to begin forging brain–cognition connections. This is not the case in memory research. The extremely wide range of neuroscience research on plasticity and learning (e.g., Fuster, 1995; Martinez & Kesner, 1998; Milner, Squire, & Kandel, 1998; Squire & Kandel, 1999) provides a rich set of puzzle pieces that will eventually be assembled in new ways as future theories of memory are developed. One way to consider the co-evolution of neural and cognitive theories of memory is with respect to the levels of computation, algorithm, and implementation as distinguished by Marr (1982). Explanations restricted to one level can be important (Dror & Gallogly, 1999). On the other hand, a complete understanding of memory will require explanation at all levels, along with systematic mappings between levels. No matter how the levels are conceptualized, or how many are distinguished, the levels are inherently interdependent, at least to some extent. An accurate conception of neural plasticity at cellular and molecular levels must ultimately be an important part of a comprehensive understanding of human memory. Yet, it is difficult to bring most of this evidence to bear on cognitive theories of memory at present.

Moreover, quite different criteria apply towards achieving the goal of understanding neural substrates versus the goal of understanding cognitive structure. For example, an empirical connection between a brain region and a specific memory function may constitute a step forward in understanding neural substrates, but may have no impact whatsoever on understanding cognitive structure. Suppose that two putatively distinct memory functions were implemented in two different brain regions. This finding could be a trivial one for cognitive theorizing if the computations and representations in the two regions were identical, merely situated in two different physical locations for arbitrary reasons. On the other hand, an anatomical separation between two memory functions *may* correspond to a fundamental psychological distinction between them, as described in the next section. In general, empirical brain–behavior associations or dissociations are most useful for understanding cognitive structure when a fairly developed theoretical framework for the evidence is already available. It can be especially useful to relate the proposed function of a network of neurons to compatible evidence about other cognitive roles played by the same network. Furthermore, when a brain region plays a role in multiple cognitive functions, a more complete understanding of the interrelationships between diverse cognitive functions can be sought.

In sum, cognitive theories can be reinforced and extended by combining them with empirically supported characterizations of the neural implementation of relevant processes. This statement is compatible with a rationale for combining cognitive and neuroscientific approaches enunciated by philosopher Owen Flanagan (1992). First, he postulated that behavioral facts alone will not provide sufficient empirical constraints on cognitive theories, and that "psychological explanations need to be constrained by knowledge about the brain" (Flanagan, 1992, p. 12). But he also suggested that neuroscience cannot generate progress in understanding the mind without adequate emphasis on the psychological phenomena themselves. The goal of understanding cognition is too lofty for either cognitive science or neuroscience alone; it requires both. Sound cognitive theorizing is required if attempts to understand the neural implementation of cognitive functions are to be successful. And a sound understanding of neural implementations is required for cognitive theorizing to be successful in the long term. Therefore, neural and cognitive advances can best be pursued together.

II. The Neural Implementation of Declarative Memory

Mental disorders due to brain damage often provide striking demonstrations of the interrelations between mind and brain. Neuropsychological studies of patients with amnesia have been especially useful for charting connections between memory and the brain. This usefulness is a fortuitous by-product of the fact that the amnesic deficit can be highly selective. An amnesic deficit is selective when it occurs together with a vast array of preserved cognitive functions, including some memory functions. Accordingly, evidence from amnesia has been widely used to develop hypotheses about the fundamental structure of memory. In particular, *declarative memory* has been defined behaviorally as the type of memory required for recalling and recognizing facts and events and for experiencing conscious recollection under such circumstances (Squire, 1987). Ample neuropsychological evidence supports the classification of declarative memory as distinct from other types of memory. Nevertheless, the precise nature of declarative memory remains to be elucidated.

The key empirical support for distinguishing between declarative and nondeclarative memory consists of a set of dissociations, wherein amnesic patients demonstrate poor memory when tested by recall or recognition but not when tested using various *implicit memory tests,* which are memory tests that make no reference to prior learning episodes. These two classes of memory phenomena can thus be distinguished:

1. *Conscious recollection*—when one brings to mind some prior event or some factual knowledge, with the awareness of retrieving a memory.
2. *Perceptual priming*—when behavior is changed in certain circumstances pertaining to a specific perceptual event, as the result of prior experience, and with no necessary experience of recollection.

One example of an implicit memory test used to show preserved perceptual priming in amnesia is the word-identification test (Cermak, Talbot, Chandler, & Wolbarst, 1985; Haist, Musen, & Squire, 1991; Hamann, Squire, & Schacter, 1995; Paller, Mayes, McDermott, Pickering, & Meudell, 1991). In this test, subjects attempt to read words presented in a degraded manner. Perceptual priming can be observed when identification is superior for words that also appeared in a study phase preceding the word-identification test. Although amnesic patients generally show normal priming in the word-identification test, they perform poorly when asked to recognize whether those words were presented earlier (Figure 1). Preserved priming in amnesia has also been verified with a wide variety of other implicit memory tests in a large literature on the topic (Moscovitch, Vriezen, & Goshen-Gottstein, 1993; Schacter, Chiu, & Ochsner, 1993; Shimamura, 1986, 1993). Although such dissociations can arise for artifactual reasons, alternative explanations based on these artifacts cannot explain the bulk of the evidence of preserved priming in amnesia (Hamann et al., 1995; Hamann & Squire, 1997; Squire, Hamann, & Schacter, 1996). Other types of memory shown to be preserved in amnesia include motor skills, cognitive skills, simple classical conditioning, habits, artificial grammar learning, category learning, nonassociative learning, and working memory (Gabrieli, 1998; Schacter & Tulving, 1994; Squire, 1992; Squire & Knowlton, 2000; Squire & Paller, 2000).

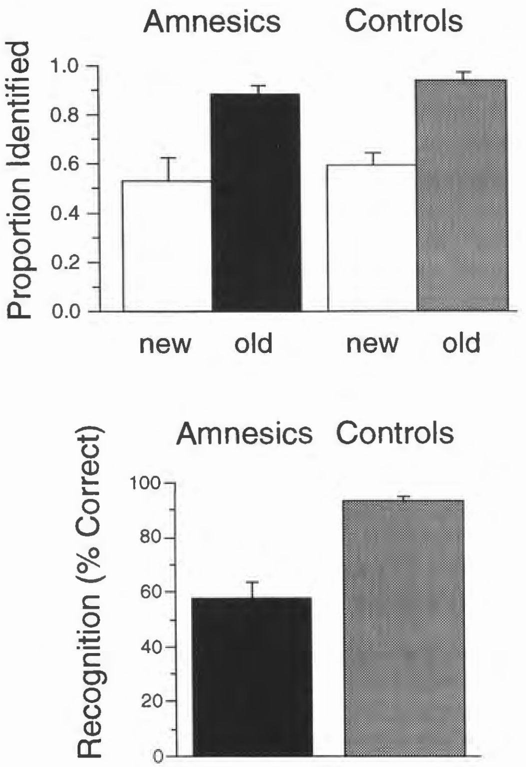

Fig. 1. Memory performance in amnesic patients and age-matched control subjects on implicit and explicit memory tests. Patients with amnesia exhibited normal word-identification priming (top) and impaired three-alternative recognition for the same words (bottom). Figure adapted from Paller et al. (1991).

These are remarkable findings because they support the notion that memory should be conceived of as encompassing a set of functions, not just one ability. Furthermore, the fact that such distinctions are honored by neuroanatomical boundaries bodes well for further neurocognitive exploration. Imagine instead an alternative state of affairs such that declarative and nondeclarative memory depend on exactly the same neuroanatomical regions at some gross level of analysis. There might be no simple way in which declarative memory could be disrupted without also disrupting nondeclarative memory. We could still be dealing with a fundamental distinction, but if the relevant memory functions were implemented in intermingled neural tissue it would be more difficult to clarify the neural basis of the distinction. The discovery that declarative and nondeclarative memory are anatomically distinct opens the door for further investigations that can both clarify the neural bases of the distinction and elucidate the cognitive processes specifically associated with each type of memory. We can thus envision ways to pursue memory theories that address both cognitive structure and neural implementation.

According to theoretical formulations put forward by countless memory theorists (e.g., see Mayes & Downes, 1997), the neural dysfunction in amnesic patients disrupts declarative memory but leaves other types of memory entirely intact. Exactly why declarative memory has this status remains an issue of continued investigation. Nonetheless, a key generalization is that when memory breaks down in amnesia, recollection is partially disrupted but certain types of priming are preserved. By juxtaposing recollection and priming, we can learn about how they differ from each other, in both their psychological and neural facets, and thus come to a better understanding of each on its own. For example, brain potentials that follow the time course of these two memory phenomena may provide a way to monitor relevant cognitive processes and study their neural substrates. Research of this sort may ultimately support attempts to describe the enigmatic border between conscious and unconscious mental events in neural terms.

A fundamental speculation about declarative memory is that the requisite information storage takes place within neocortical areas dedicated for processing the particular type of information in question (Squire & Paller, 2000). Memories are not all stored in a unitary memory storehouse in the brain. Instead, facial memories are stored in cortical areas where facial information is represented, verbal memories where verbal information is represented, and so on. Memory storage in the cortex generally follows functional specialization in the cortex. Yet, the memory dysfunction of amnesia cuts across all sensory modalities, while at the same time it does not disrupt perceptual abilities. The amnesic impairment is global in that it encompasses memories based on all sorts of information, but it is also focal in that it is restricted to declarative memory. This pattern of memory breakdown provides important clues for understanding the neural and cognitive nature of memory. In fact, there is a substantial consensus among scientists studying memory disorders that the central problem is generally in storing declarative memories rather than in encoding or retrieving them per se.

I will now present one specific conceptualization of this memory storage problem, based on some ideas I proposed earlier (Paller, 1997). First, amnesia can result from a defect in a special sort of *consolidation* process whereby enduring declarative memories are stored in the cerebral cortex. This consolidation process is required because the elements of a declarative memory are not easily held together, due to their anatomical isolation. Consolidation entails interactions between the cerebral cortex and two key brain areas, the medial temporal region and the medial diencephalon (Figure 2). The brain dysfunction in amnesia most commonly lies in one or the other of these two key areas, as structural neuroimaging, functional neuroimaging, and post mortem histology have shown.

Declarative memories characteristically depend on multiple *neuronal ensembles* (Hebb, 1949) that represent different high-level perceptual, cognitive, and emotional attributes processed in functionally distinct cortical regions. The experience of a fact or event in the present moment, as in immediate memory or working memory, can be achieved when one such set of distributed neuronal ensembles is activated under the control of prefrontal networks. Furthermore, this set of neuronal ensembles can become temporarily connected via cortico-thalamic and cortico-hippocampal networks. This temporary linking function is, in some cases, ultimately replaced by new neocortical representations, instantiated by "coherence ensembles" (Paller, 1997), which are located in temporal lobe regions near the hippocampus[1]. The central function of these newly formed neuronal ensembles is to provide coherence to the dispersed neocortical representation. Enduring declarative memories are, by this account, characteristically composed of a set of distributed neocortical ensembles plus associated coherence ensembles (Figure 3).

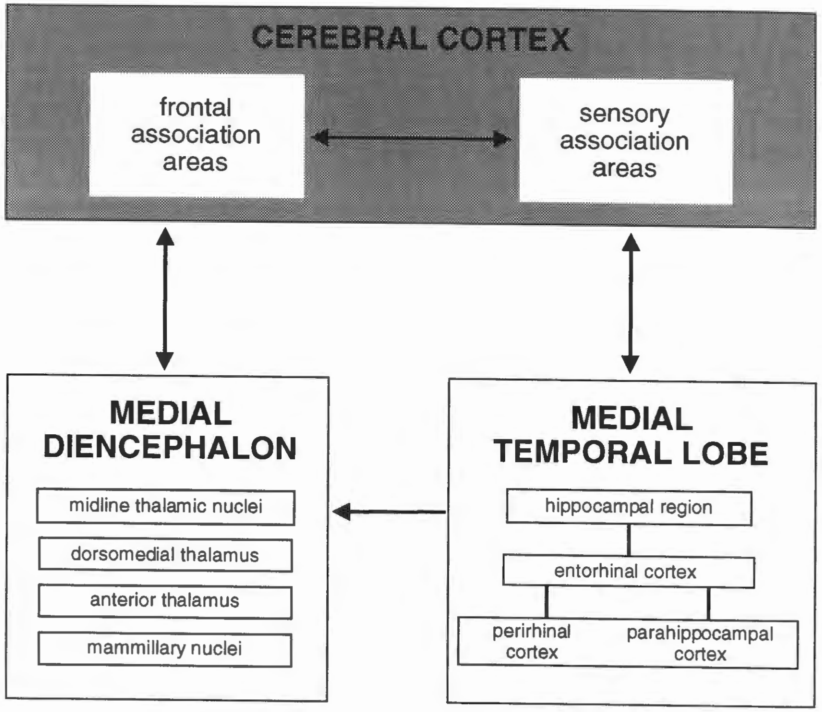

Fig. 2. Neuroanatomical regions involved in the storage of declarative memories. Figure adapted from Squire and Paller (2000).

Consolidation fundamentally entails the repeated activation of this set of neocortical storage sites, thereby mediating memory retrieval, associations with other memories, and the formation of an enduring declarative memory. These several events that comprise consolidation can proceed whether or not the individual is intending to memorize or rehearse the memory, such as during the experience of related events or during sleep. Other aspects of this theoretical formulation have been described in detail elsewhere (Paller, 1997); for present purposes a central implication is that declarative memory and priming can now be given these tentative neurobiological definitions:

1. Declarative memory is a type of neocortical memory in which the relevant plasticity occurs *across* many neocortical zones, and storage requires a special consolidation process that is unique to this type of dispersed neocortical memory.
2. Priming is a type of neocortical memory in which the relevant plasticity occurs *within* a single neocortical zone.

Although priming has most commonly been investigated using single items such as words, sometimes pairs of items have been used instead. In such cases, priming may rely on associations among separate representations. Such new associations might depend on plasticity across multiple neocortical zones rather than merely within-zone plasticity. According to the conceptualization outlined above, this would require consolidation. Indeed, implicit memory tests that tax priming for new associations often reveal impairments in amnesic patients (Cermak, Bleich, & Blackford, 1988; Chun & Phelps, 1999; Mayes & Gooding, 1989; Paller & Mayes, 1994; Schacter & Graf, 1986; Shimamura & Squire, 1989). Exceptions to this generalization (Gabrieli, Keane, Zarella, & Poldrack, 1997; Musen & Squire, 1993) may reflect the use of unitized representations such that

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[1] The most severe cases of amnesia are caused by damage to these temporal lobe regions plus the hippocampus. In contrast, damage to these temporal lobe regions alone can lead to semantic dementia, in which remote memories may be disrupted more than recent memories (Hodges & Graham, 1998). Speculatively, damage to a circumscribed portion of these regions with relative sparing of the hippocampus and some adjacent temporal cortex may cause a focal retrograde amnesia (Kapur, 1993; Markowitsch, 1995), such that the patient exhibits excessive retrograde impairments along with a preserved ability to form new declarative memories.

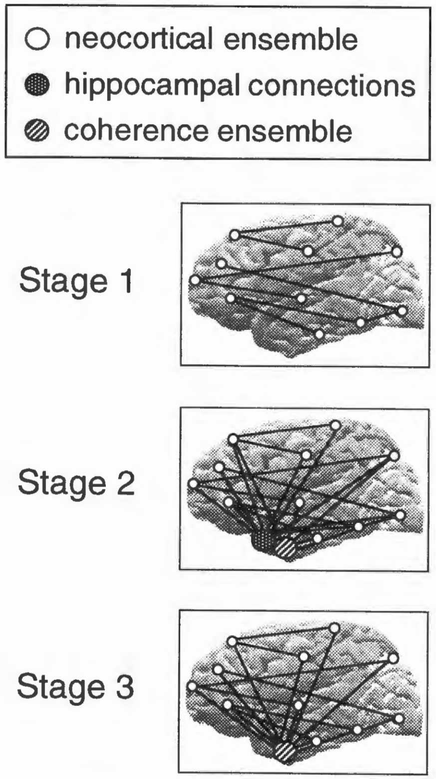

Fig. 3. Figurative depiction of the stages of consolidation of dispersed neocortical memories. In stage 1, a fact or event is encoded via representations that involve multiple cortical regions, based on working memory processes controlled by prefrontal cortex. At about the same time, in stage 2, this dispersed representation begins to make contact with neurons in the medial temporal region. Hippocampal connections rapidly become part of a newly formed network so that the dispersed cortical fragments can remain connected beyond the span of immediate memory. In addition, coherence ensembles are formed in entorhinal, perirhinal, and parahippocampal cortex, and possibly in adjacent cortical regions, and these become part of the network. Connections become strengthened as the memory is reactivated on subsequent occasions, while coherence ensembles develop a central role as they take on gestalt-like aspects of the memory and its relationship to other memories. Coherence ensembles thus function to maintain cohesiveness among the various parts of the declarative memory. In stage 3, coherence ensembles can take part in the reactivation of the dispersed neocortical memory without any necessary contribution from hippocampal connections.

plasticity within single neocortical zones is operative. In short, implicit memory tests do not always show normal priming in amnesia. For normal priming to be observed in amnesia, performance in healthy individuals

must not be mediated by recall or recognition, and performance must not depend on new associations represented across distinct cortical zones.

The dissociation between recollection and priming in amnesia can now be recast in neurobiological terms—recollection is impaired due to consolidation failure following disruption of either cortico-thalamic or cortico-hippocampal networks, whereas priming due to plasticity within single neocortical zones is preserved. In attempting to tie together psychological and biological facets of amnesia, this conceptualization portrays the beginnings of a neurocognitive theory of declarative memory and priming in healthy individuals. Given the rapid growth of cognitive neuroscience in recent years, there is reason to be optimistic that this theory can be developed further, specified in increasingly precise detail, and put to empirical test. But a critical step will be to identify measures of the relevant memory functions in human subjects.

III. Electrophysiological Measures of Recollection

Given these hypotheses about memory derived from neuropsychological research, I will now explore how relevant evidence can be obtained by measuring brain activity in healthy individuals. In particular, I will focus on measures of brain activity called event-related potentials (ERPs), which are extracted from the electroencephalogram (EEG) using signal-averaging methods. Many aspects of this treatment also apply to work with other methodologies that provide evidence about brain activity during cognitive functions, including positron emission tomography (PET), functional magnetic resonance imaging (fMRI), magnetoencephalography (MEG), and transcranial magnetic stimulation (TMS). Noninvasive ERP recordings from the scalp reflect the summation of electrical activity generated in various brain regions, activity which summates by virtue of factors such as the spatial alignment of neurons and the synchrony of neural activity (Kutas & Dale, 1997). The present discussion of ERPs and memory has a limited scope (for more extensive reviews of the literature, see Johnson, 1995; Kutas, 1988; Rugg, 1995).

ERPs arguably provide measures of memory processes that can aid the development and testing of theories of human memory in several ways. ERPs have been recorded during various sorts of recognition tests, and results suggest that differential ERP responses to old and new items may be useful for studying retrieval (e.g., Friedman, 1990; Johnson, Pfefferbaum, & Kopell, 1985; Karis, Fabiani, & Donchin, 1984; Neville, Kutas, Chesney, & Schmidt, 1986; Paller, Kutas, & Mayes, 1987; Rubin & McAdam, 1972; Rugg & Nagy, 1989; Sanquist, Rohrbaugh, Syndulko, & Lindsley, 1980;

Warren, 1980). Although not emphasized here, other electroencephalographic phenomena have also been linked to memory functions, including slow potentials (Rösler, Heil, & Roder, 1997) and measures in the frequency domain (Klimesch, 1999).

In ERP experiments with visual words, responses to old words have tended to be more positive than responses to new words about 400 to 800 ms after word onset (Figure 4). ERP studies of recognition have also been conducted with nonverbal stimuli such as simple object drawings (e.g., Friedman & Sutton, 1987) and faces (e.g., Barrett, Rugg, & Perrett, 1988; Smith & Halgren, 1987). In one experiment, ERPs were recorded from subjects while they viewed color slides depicting a variety of people, places, and paintings (Neville, Snyder, Woods, & Galambos, 1982). Following ERP recordings, subjects were shown each slide a second time and asked whether they had recognized it during its initial exposure. An average of 11% of the slides fell into this category, and ERPs to these recognized slides were considerably more positive than ERPs to unrecognized slides, particularly at around 400 ms. This result parallels findings from various other experiments in which items recognized from a presentation earlier in the experiment elicited ERPs that were more positive than ERPs to new items. These reports of *old-new ERP differences* provide a good foundation for the suggestion that recognition processes are measurable using ERPs.[2]

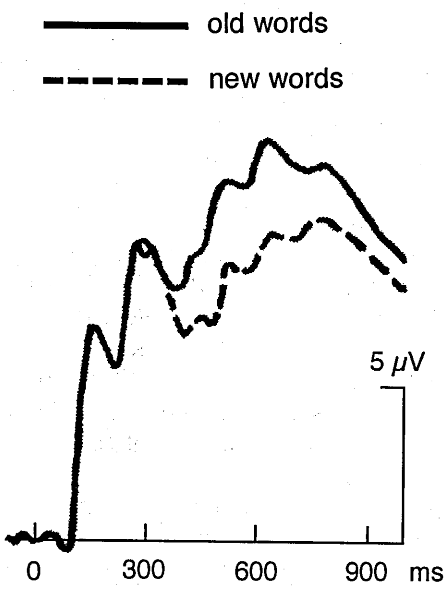

Fig. 4. An example of an old–new ERP difference (also known as an ERP repetition effect) obtained during a yes–no recognition test. The response to old words was more positive than the response to new words, beginning about 400 ms after word onset (from results obtained by Paller et al., 1987). Recordings were made from the midline parietal scalp location, and positive potentials are shown as upward deflections.

Before accepting the claim that ERPs tap processes central to recognition, however, we must consider several features of typical recognition paradigms that cloud the issue. First, both the time to make a recognition judgment and the confidence with which it is made may differ considerably between old and new items.[3] Second, the fact that subjects are required to detect recognized items may call into play target-detection operations that differ for old and new items, in that only the former are targets. Third, the subjective probability of old and new items may differ, whether or not actual stimulus probabilities are matched. All of these factors are known to influence ERPs, so these confounding factors are particularly worrisome. In short, it can be problematic to distinguish electrophysiological (or other physiological) effects due to these nonspecific factors from effects due to recognition per se. Likewise, multiple sorts of retrieval-related processes can be difficult to investigate when limited to old–new comparisons (e.g., Rugg & Wilding, 2000). Furthermore, and most important in the present context, simply comparing old and new items in a recognition paradigm does not take into account the idea that both recollection and priming occur in such a situation.

Although several lines of evidence are consistent with the hypothesis that ERPs are sensitive to recognition processes, much of the early evidence fell short of being conclusive. Johnson and colleagues (Johnson et al., 1985; Johnson, Kreiter, Russo, & Zhu, 1998) showed that ERPs correlated with

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[2] ERPs have also been used to show that neural events at the time information is first encoded are predictive of whether they will be remembered later. The phenomenon of an ERP *Difference* computed as a function of later *memory* performance, sometimes called *Dm,* has been observed with explicit memory tests such as recall and recognition (Fabiani, Karis, & Donchin, 1986; Karis et al., 1984; Paller, 1990; Paller et al., 1987; Paller, McCarthy, & Wood, 1988; Sanquist et al., 1980) but not with implicit memory tests such as stem completion or word identification (Paller, 1990; Paller & Kutas, 1992). More recently, such effects have been observed with fMRI (Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Fernández et al., 1998; Wagner et al., 1998), with event-related EEG synchronization (Klimesch, 1999), with EEG coherence measures (Weiss & Rappelsberger, 2000), and with intracranial ERP recordings in the medial temporal region (Fernández et al., 1999).

[3] In one experiment, for example, ERPs were averaged separately according to confidence measures (an analysis reported by Paller, 1993, of data collected by Paller, Kutas, & Mayes, 1987). ERPs were more positive for words categorized with high confidence than with low confidence. In fact, ERPs in other paradigms are similarly correlated with decision confidence (Hillyard, Squires, Bauer, & Lindsay, 1971; Ruchkin & Sutton, 1978). Confounds with recognition confidence can thus contribute to observed old–new ERP differences, particularly when hits to old items are more confident than correct rejections to new items. In addition, confidence judgments may be insufficiently sensitive to ameliorate this problem.

increases in memory strength as study words were repeated, which would be expected for an ERP correlate of recognition strength. Bentin and colleagues (Bentin & Moscovitch, 1990; Bentin, Moscovitch, & Heth, 1992) recorded old–new ERP differences and proposed that ERPs are sensitive to both implicit and explicit aspects of memory performance. However, the methods used were insufficient for disentangling these different processes. Smith and Halgren (1989) interpreted their ERP results in terms of a distinction between two separate bases for recognition judgments, familiarity based on memory strength and contextual retrieval (Atkinson & Juola, 1973; Jacoby & Dallas, 1981; Mandler, 1980). Lists of 20 abstract words were arranged such that the same 10 words occurred in every list, and subjects were instructed to press a button whenever one of these repeating words was presented. Recognition accuracy increased across the six lists in healthy individuals and in patients with unilateral anterior temporal lobectomies (performed for relief of medically intractable epilepsy). Smith and Halgren (1989) suggested that increases in memory strength were normal in all patients, but that the ability of patients with left-hemisphere excisions to use contextual retrieval was compromised and that this explained attenuated old–new ERP differences that were found in those individuals. In other words, old–new ERP differences were thought to reflect contextual retrieval. This conclusion was not endorsed by the authors of a similar study of epileptic patients (Rugg, Roberts, Potter, Pickles, & Nagy, 1991), who found no relationship between the magnitude of old–new ERP effects and verbal memory performance.

An alternative position was advocated by Rugg and colleagues, who used several lines of evidence to argue that old–new ERP differences reflect *relative familiarity* and not recollection. The central assumption, from two-process models of recognition, was that relative familiarity (i.e., a discrepancy between the level of familiarity cued by an item and the level of familiarity that the individual would expect a priori) can function as a basis for recognition judgments. According to Jacoby and Dallas (1981), for example, familiarity can be based on fluent perceptual processing of repeated items. In one study, injections of the anticholinergic agent scopolamine were found to produce a decrement in recognition performance along with an increase in old–new ERP differences (Potter, Pickles, Roberts, & Rugg, 1992). The authors suggested that the drug had a detrimental effect on recollection that coincided with an increase in the extent to which recognition judgments were based on relative familiarity (i.e., the converse of the hypothesis of Smith and Halgren, 1989). In other experiments, the finding that old–new ERP differences were apparent for low-frequency words but not for high-frequency words was interpreted in relation to the idea that low-frequency words give rise to a higher level of relative familiarity, an idea that may also explain the recognition advantage for such words (Rugg, 1990; Rugg & Doyle, 1992). However, if we grant that recognized low-frequency words also tend to engage more recollection (e.g., Gardiner & Java, 1990), this evidence is equivocal with respect to associating ERPs with familiarity versus recollection.

Conclusively determining whether or not ERPs can be linked to recollection versus other factors required a different empirical approach. In an attempt to isolate brain waves specific to recollection, Paller and Kutas (1992) introduced a procedure based on producing behavioral dissociations between recollection and priming. Instead of only comparing ERPs to old versus new words, ERPs were compared between different types of old words presented during an implicit memory test, the word-identification test. A levels-of-processing manipulation at study was used to produce a memory dissociation of the sort previously demonstrated by Jacoby and Dallas (1981). When subjects study words by focusing on word meaning for one set of words and letter identity for another set of words, the two sets of words are generally associated with different levels of recall performance but similar levels of priming (Richardson-Klavehn & Bjork, 1988; Roediger & McDermott, 1993; but see Bentin, Moscovitch, & Nirhod, 1998; Challis, Velichkovsky, & Craik, 1996; Richardson-Klavehn & Gardiner, 1998). Of course, memory tests cannot be relied on for absolutely pure measures of underlying memory phenomena (i.e., memory tests are not process-pure). Nonetheless, reliable dissociations between certain priming tests and explicit memory tests provide a key ingredient for a convincing interpretation of the ERP findings. The two types of studied words under scrutiny differed in the extent to which recollection was provoked, but they were the same with respect to (a) physical stimulus characteristics, by virtue of the counterbalanced design, (b) the behavioral responses made in the implicit memory test, and (c) the magnitude of priming. Accordingly, we hypothesized that the ERP difference wave was an electrophysiological correlate of recollection, distinct from the influence of priming or other confounding factors. These results constitute the first published evidence to strongly support the hypothesis that the subjective experience of recollection can be monitored via measures of electrical activity of the brain (see also, Düzel, Yonelinas, Mangun, Heinze, & Tulving, 1997; Rugg, Mark, Wall, Schloerscheidt, Birch, & Allan, 1998; Smith, 1993; Smith & Guster, 1993; Wilding, Doyle, & Rugg, 1995).

This hypothesis was supported by results from several follow-up experiments. First, a variation of the original design was used along with a between-subjects manipulation of the extent to which conscious recollection occurred (Paller, Kutas, & McIsaac, 1995). Results substantiated the association between recollection and the ERP difference computed between the two study tasks, and also showed that it was not specific to the particular circumstances in the initial experiment. Consistent with this conclusion, abnormal ERP responses were observed when the same experimental paradigm was used with elderly participants with mild declarative memory impairments (Joyce, Paller, McIsaac, & Kutas, 1998), and when a related paradigm was used with amnesic patients with moderate to severe declarative memory impairments (Olichney et al., in press). Indeed, Olichney and colleagues found that the magnitude of late positive ERP differences was correlated with the extent of memory impairment in these patients, either measured via memory tests for the words used in the experiment or via standardized neuropsychological tests.

Other experiments showed that ERP correlates of recollection can also be elicited by photographs of faces (Paller, Bozic, Ranganath, Grabowecky, & Yamada, 1999; Paller, Gonsalves, Grabowecky, Bozic, & Yamada, 2000). In these experiments, participants were first asked to memorize a set of faces that were each accompanied by a voice simulating the voice of that individual (e.g., "I'm Alison and I won the Boston Marathon twice"). In a test phase, ERPs to these faces ("remember faces") showed reliable differences in comparison to ERPs to new faces as well as to ERPs to faces that had been presented in the study phase without voices and with instructions to forget ("forget faces"). Importantly, results from a separate behavioral experiment showed that priming did not differ between the two types of studied faces, whereas remember faces were later recognized much more accurately. The ERP difference between the two types of studied faces can therefore be taken as a neural correlate of recollection, disentangled from ERP correlates of priming. Of course, it will also be necessary to specify the full range of cognitive processes that contribute to recollective experience in these situations. In this regard, we have speculated that retrieval occurs through interactions between frontal and posterior cortical areas, and this speculation has been supported by combined fMRI and ERP evidence obtained using the same general paradigm (Paller et al., 2000). Furthermore, other ERP results likewise suggest that frontal regions are particularly important for successful episodic retrieval (Ranganath & Paller, 1999a, 1999b, 2000), as do many recent results from neuroimaging and neuropsychology (see Nolde, Johnson, & Raye, 1998; Rugg & Wilding, 2000; Shimamura, 1996).

A strategy analogous to the one described above for visual stimuli has also been used in the auditory modality (Gonsalves & Paller, 2000). Spoken words were again presented under two different study conditions using a levels-of-processing procedure. Priming of lexical decision response time was the same across different study conditions, whereas recognition was not. We interpreted test-phase ERPs that differed due to study conditions as electrical reflections of the visual imagery engaged when the words were heard. This differential imagery took place both during study and test, even though the test condition did not require it. Indeed, we speculated that our electrophysiological measures reflected the recapitulation of this visual imagery, a prominent factor supporting accurate word recognition.

In sum, studies of old-new ERP differences initially led to divergent hypotheses about relationships between ERPs and memory retrieval, whereas subsequent studies succeeded in isolating ERP correlates of recollective processing. Due to the fact that both recollection and priming tend to occur when studied items are presented in a memory test, conventional analyses of old–new ERP effects are typically equivocal with respect to isolating ERPs associated with one type of memory or the other. Successful demonstrations of ERP correlates of recollection required (a) recording ERPs during recognition as well as in situations wherein subjects were not required to make overt recognition responses; (b) comparing study conditions that differentially influenced declarative memory and priming; and (c) including behavioral measures to confirm the memory dissociations. The idea that the neural events responsible for conscious recollection can be observed as they occur is important because such observations should prove helpful for testing theories about the neurophysiology of memory. Moreover, this approach can potentially enrich our understanding of *both* the cognitive structure and the neural substrates of memory.

IV. Electrophysiological Measures of Perceptual Priming

So far I have focused on processes associated with recollection, but it is also illuminating to consider neural correlates of priming. The same experimental approach has been used, here taking advantage of manipulations that influenced priming more than recollection. In one experiment, words were displayed at study either as complete words or by showing one letter at a time in quick succession (Paller, Kutas, & McIsaac, 1998). Priming was enhanced in the former relative to the latter condition, whereas recognition was relatively unaffected. ERPs corresponding to this differential priming were recorded during the priming test, when all words were displayed as complete words. This ERP correlate of priming was interpreted as a reflection of differential processing of visual word form (i.e., words represented as whole units), given that so many other aspects of word processing were matched in the two study conditions. However, this ERP correlate of priming thus reflects just one subtle memory phenomenon, not all possible consequences of prior experience with a word. The ERP correlate of visual word-form priming recorded by Paller and colleagues (1998) differed from

ERP correlates of recollection cited above in that it occurred slightly earlier and had a focal topography centered at occipital scalp locations. Similar results were found in a subsequent experiment in which priming was manipulated by presenting words either spelled forwards or backwards (Paller & Gross, 1998). Results from these two experiments together suggest that ERPs can provide online measures to monitor priming (see also, Joyce, Paller, Schwartz, & Kutas, 1999; Rugg et al., 1998). In addition, these ERP correlates of priming confirm the necessity of valid experimental procedures to disentangle ERP correlates of implicit and explicit memory.

Perceptual priming is known to occur even when an individual cannot explicitly distinguish between old and new items, and it has been related to the concept of unconscious memory. Speculations about unconscious memory are plentiful—from Freud's explorations of the unconscious to current concerns with repressed memories—but direct measurements of unconscious memory are rare and controversial. Possible electrophysiological correlates of priming have also been revealed in recordings from single neurons in monkey visual cortex (Desimone, 1996). Some neurons in ventral temporal areas, in particular, tend to show reduced responses during stimulus repetitions, or "repetition suppression." Neuroimaging in humans also suggests that priming may result from decreased neural activity following perceptual learning, which may be the essence of efficient perceptual processing (Wiggs & Martin, 1998).

A direct comparison between an electrophysiological correlate of recollection and an electrophysiological correlate of perceptual priming is shown in Figure 5. These measures of brain events underlying recollection and priming provide new empirical footholds for theoretical advances regarding the critical differences between memories that are accessible to consciousness and those that are not—and perhaps between conscious and unconscious events in general.

V. Conclusions: Cognitive Neuroscience and Human Memory

Neuropsychological studies of amnesia have shown which brain areas are essential for various memory functions, but moving ahead to seek a comprehensive understanding of how these functions are implemented in the brain, and of their precise cognitive structure, will require an alliance among multiple empirical approaches, both in healthy and brain-damaged people. The usefulness of electrophysiological and functional neuroimaging techniques in this regard will require experimental designs that take optimal advantage of the spatial and temporal resolution provided by each method. Not only must research in this area take into account the strengths and limitations of each technique for measuring brain function, but the successful application of these techniques depends critically on whether subjects' cognitive activities can be adequately controlled.

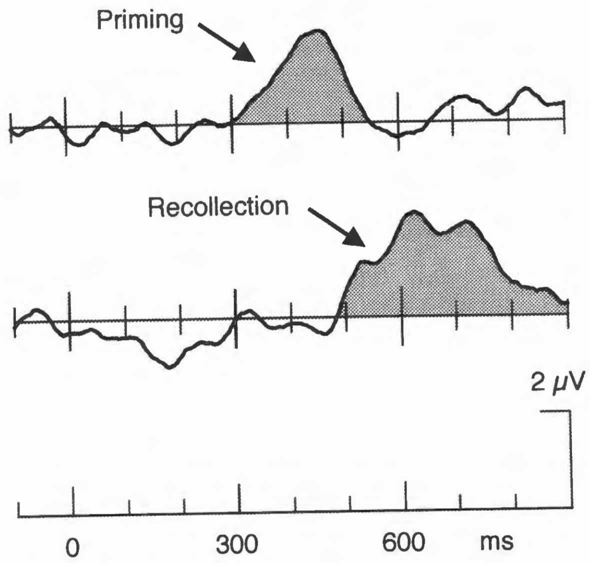

Fig. 5. Brain potentials specifically associated with visual word-form priming and recollection. The upper wave form was computed by subtracting brain potentials elicited by words previously viewed forwards or backwards; priming was greater in the former compared to the latter condition (Paller & Gross, 1998). The lower wave form was computed by subtracting brain potentials elicited by words previously studied in an imagery task versus an orthographic task; recollection was stronger in the former compared to the latter condition (Paller & Kutas, 1992). Recordings were made from the midline parietal scalp location, and positive potentials are shown as upward deflections.

In several experiments, results have supported the speculation that a particular brain potential provided an objective measure of an unobservable phenomenon, the conscious experience of retrieving a memory. This electrophysiological correlate of conscious recollection contrasts with other findings showing that different brain potentials are associated with perceptual priming of visual word form. The further development of such contrasts between recollection and priming using this methodology should lead to a rich source of evidence pertaining to the neural implementation of these distinct memory functions.

Studies of the neural bases of human memory have the potential for expanding the insights gained from prior cognitive and neuropsychological studies of memory. Contrasts between recollection and priming, in particular, have launched massive theoretical development. Although more work will be required to adequately test and develop these ideas, a tenable working hypothesis is that recollection and priming can be characterized as different types of neocortical memory dependent on distinct neurophysiological mechanisms. Priming appears to depend on isolated instances of neocortical plasticity such that subsequent processing in one or more cortical regions is altered. In contrast, recollection requires the formation of links among sets of neocortical regions in the service of creating an enduring declarative memory. The aforementioned evidence that ERPs can be used to monitor processes associated with recollection, as well as processes associated with priming, suggests that this approach will be useful for developing more fine-grained hypotheses about the neurophysiology of the two types of memory.

Ultimately, such efforts to understand the neural bases of human memory will shed light not only on the nature and organization of memory processes in the brain, but also on the subjective experience of conscious recollection. However, understanding the neural implementation of memory functions and understanding the cognitive structure of memory should ideally be conceived not as two separate goals. These are fundamentally two parts of the same endeavor. Advances in understanding neural implementations turn on the accuracy of assumptions about cognitive structure. Advances in understanding cognition, as argued above, must ultimately be grounded in an accurate conception of the neural substrates of cognition. Seeking to understand human memory is a colossal challenge and it requires the full force of both cognitive science and brain science.

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