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Cognitive neuroscience of episodic memory encoding

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Abstract

This paper presents a cognitive neuroscientific perspective on how human episodic memories are formed. Convergent evidence from multiple brain imaging studies using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) suggests a role for frontal cortex in episodic memory encoding. Activity levels within frontal cortex can predict episodic memory encoding across a wide range of behavioral manipulations known to influence memory performance, such as those present during levels of processing and divided attention manipulations. Activity levels within specific frontal and medial temporal regions can even predict, on an item by item basis, whether an episodic memory is likely to form. Furthermore, separate frontal regions appear to participate in supplying code-specific information, including distinct regions which process semantic attributes of verbal information as well as right-lateralized regions which process nonverbal information. We hypothesize that activity within these multiple frontal regions provides a functional influence (input) to medical temporal regions that bind the information together into a lasting episodic memory trace. © 2000 Elsevier Science B.V. All rights reserved.

The question addressed in this paper is simple: why do certain events and experiences form episodic memories? This question can be answered at different levels of description. At one level, theories from cognitive psychology provide an account of

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how certain forms of processing facilitate episodic memory formation, outlining the conditions necessary to promote these forms of processing and the many variables that may influence retrieval of episodic memories after they have formed. At another level, evidence from neuroscience provides information about the neural structures that support encoding, and characterizes the operations carried out by these neural structures. The view of encoding presented here reflects a cognitive neuroscience approach that relates these two levels of description. The aim is to understand how encoding and its behavioral manifestations arise from the workings of underlying neural structures.

What follows is a review of recent results from brain imaging studies that suggests a cognitive neuroscience theory of how episodic memories form and why some experiences are more likely than others to establish a lasting memory trace. While the theory is incomplete, there is good evidence supporting the notion that certain types of encoding processes may onto neural activity within specific brain regions, and that evidence from neuroscience can inform and constrain studies of behavior and vice versa. Although several brain regions are likely to be involved in episodic memory formation, in this paper particular focus is placed on (1) the role of the frontal cortex in episodic memory encoding, and (2) how frontal regions may interact with medical temporal regions that play a well-established role in episodic (and semantic) memory formation. The main conclusion drawn is that for an episodic memory to form an event must encourage elaboration of information within specific frontal regions that provide a critical input to medical temporal cortex. Components of these ideas have been presented previously (e.g., for a highly overlapping explication see Buckner, Kelley, & Petersen, 1999; Buckner, 1999).

1. Brain imaging studies suggest specific left frontal regions contribute to verbal episodic encoding

The majority of data about human episodic memory encoding comes from studies using verbal materials. One manner of encoding words into episodic memory is *intentional* memorization. Brain imaging studies, using functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) have consistently demonstrated that specific regions within left frontal cortex are active when subjects intentionally memorize words (Fletcher et al., 1995; Kapur et al., 1996; Kelley et al., 1998).

However, many instances of episodic memory formation in everyday life occur *incidentally*, without any intention to remember. As studies in cognitive psychology have shown (cf. Postman, 1964; Hyde & Jenkins, 1973; Craik & Lockhart, 1972), episodic memories can form as a byproduct of certain kinds of information processing, independent of the intent to remember. For example, words that are deeply processed in terms of their meaning and how they relate to other items in memory are better remembered than words processed in a shallow fashion in which only surface characteristics are examined – the well-known levels of processing effect (e.g., Craik & Lockhart, 1972). Frontal regions active during *intentional* memorization are also active during behavioral manipulations that *incidentally* alter the effectiveness of memory encoding. For example, when subjects perform tasks requiring meaning-based judgments on words, multiple regions within left frontal cortex are activated. Those words are remembered even though the subjects make no explicit attempt at memorization (Demb et al., 1995; Gabrieli et al., 1996; Kapur et al., 1994; Buckner & Koutstaal, 1998; Wagner et al., 1998b). By contrast, when subjects perform a shallow surface-based task, where words are judged to be in uppercase or lowercase letters, frontal activity is minimal, and memory for the words is poor.

Cognitive investigations also reveal that dividing attentional resources at the time of encoding can influence episodic memory formation. When attention is directed away from an item, that item is likely to be forgotten even if a subject is attempting to remember it (Craik et al., 1996). Consistent with this behavioral observation, one influential PET study demonstrated that adding a secondary distracting task during intentional memorization caused brain activity in frontal cortex to diminish and memory to be impaired (Fletcher et al., 1995). Thus, studies of both levels of processing and divided attention suggest a link between activity within specific frontal regions and encoding processes.

Further evidence for such a link comes from neuroimaging studies that provide insight into why some experiences are remembered while others are forgotten. Several recent imaging studies based on fMRI have demonstrated that activity within specific frontal (and sometimes medial temporal) regions can predict which specific experiences will be remembered on a moment to moment basis. The basic idea for these investigations came from a series of studies using electrical scalp recording techniques (Fabiani et al., 1986; Paller, 1990; for reviews see Rugg, 1995; Wagner, Koutstaal, & Schacter, 1999). These studies recorded scalp potentials from subjects at the time of memorization, revealing differences in the amount of activity for words which were later remembered as compared to those that were later forgotten. Developments in fMRI methods (Buckner et al., 1996; Dale & Buckner, 1997; Josephs, Turner, & Friston, 1997; Konishi et al., 1996; Kim, Richter, & Ugurbil, 1997) allowed similar phenomena to be examined with more precise spatial (anatomic) localization, providing information about the source of these memory related effects within the brain. Using event-related averaging procedures, it has been shown that the level of activity within specific left frontal regions can predict, on average, whether a word will later be remembered or forgotten (Rotte et al., 1998; Wagner et al., 1998b; Buckner et al., In press; see also Alkire, Haier, Fallon, & Cahill, 1998; Brewer, Zhao, & Gabrieli, 1998). Across these studies, subjects performed tasks encouraging semantic processing on words without any expectation of a later memory test. Then, during a later surprise episodic recognition test, those words that were remembered could be sorted and compared to those words that were forgotten, identifying neural correlates that predicted memory performance. In all instances, specific regions of frontal cortex were among those most strongly correlated with subsequent memory performance. These findings provide a compelling example of the direct link between measures of brain activity and behavioral performance in episodic memory encoding.

Frontal regions active in the studies discussed above extend across *anatomically* distinct regions of frontal cortex. Most often, increases in brain activity occur within frontal cortex near the border of motor and prefrontal cortex (located along inferior frontal gyrus dorsally near Brodmann's areas [BA] 44 and 6) and more ventral prefrontal regions (near BA 44, 45 and 47, sometimes extending into anterior BA 10). Thus, encoding related activations likely include *functionally* heterogeneous regions of frontal cortex (Buckner, Raichle, & Petersen, 1995; Buckner, 1996; Petrides & Pandya, 1994; Petrides, Alivisatos, & Evans, 1995).

Insight into the functional heterogeneity of these regions and their separate contributions to episodic encoding has recently been provided by a fMRI study of incidental encoding by Logan, Kelley, and Buckner (2000). The study involved comparison between processing tasks promoting deep (meaning-based) and shallow (phonologically-based) incidental encoding. Unlike many studies comparing deep and shallow encoding, Logan et al. (2000) constructed a situation where the shallow encoding task decision took longer, on average, than the deep encoding task decision (as measured by key-press reaction time; see Demb et al., 1995 for a similar manipulation). Regions along the dorsal extent of inferior frontal gyrus (BA 44 and/or 6) were similarly activated in both the deep and shallow encoding conditions. By contrast, the most inferior extent of inferior frontal gyrus near BA 44/45/47 was most active during deep compared to shallow encoding.

This pattern of results in the context of episodic encoding is consistent with prior notions of functional dissociation across left frontal regions (Buckner et al., 1995; Buckner, 1996; Poldrack et al., 1999). Specifically, the dorsal extent of left frontal cortex is thought to play some role in the phonological processing of verbal materials. By contrast, semantic or meaning-based elaboration upon verbal materials recruits additional regions, namely inferior and anterior portions of left frontal cortex (Buckner, 1996). Thus, dorsal [BA 44 and or 6] and inferior [BA 44/45/47] portions of frontal cortex may play distinct roles in episodic encoding, with inferior frontal regions providing the most selective association between levels of activation and episodic encoding. An intriguing possibility is that multiple frontal regions participate in verbal processing but correlate with distinct processes and/or verbal codes (e.g., lexical, phonological, semantic). Activation of BA 44/45/47 appears to occur when tasks demand elaboration upon or selection among semantic codes. Activation of inferior frontal regions may thus most selectively correlate with episodic encoding because semantic codes are among the most conductive for forming episodic memories for words (but see Morris, Bransford, & Franks, 1977; Stein, 1977 for further discussion).

In summary, the data described above suggest that the amount of activity within specific left frontal regions at the time of encoding correlates with later episodic memory performance for verbal material. Nonetheless, there are likely to be many other important factors that influence memory performance (e.g., retrieval processes) which are not captured by the above summary. Fisher and Craik (1977, p. 710) make an analogous point in the context of behavioral data, stating that "No one factor in isolation – the type of encoding, the type of cue, or the compatibility between encoding and cue – is by itself sufficient to describe performance." Similarly, we speculate that *frontal activity during encoding is necessary for successful performance on certain types of memory task, but is unlikely sufficient for predicting recollection on subsequent tests of episodic memory.*

2. Frontal contributions to nonverbal episodic encoding

Left frontal cortex has been consistently associated with encoding of verbal materials as outlined above and highlighted in several prior reviews (e.g., Tulving, Kapur, Craik, Moscovitch, & Houle, 1994; Nyberg, Cabeza, & Tulving, 1996a; Buckner, 1996). However, we are also able to remember aspects of events that are not purely verbal in nature such as the appearance of a remembered face or the intonations and accent of a remembered voice. A point of debate in the literature surrounds how we memorize these forms of nonverbal materials. Specifically, is frontal cortex involved in the memorization of nonverbal materials, and, if so, are the regions laterlized in the same manner as during verbal encoding? Cognitive theories suggest that memory formation relies on multiple kinds of information, with one important distinction being between verbal and nonverbal codes. Behavioral studies show that a picture of an object, such as a lion, is more likely to be remembered than the presentation of the word "lion" (a finding known as the *picture superiority effect*). The implication is that pictures are associated with both nonverbal (image-based) and verbal codes, while words are only associated with a verbal code (Paivio, 1986; Paivio & Csapo, 1973). Moreover, encouraging subjects to imagine which object a word represents will boost memory performance, implying that multiple codes are better than one for forming an episodic memory.

Further evidence that multiple codes contribute to memory comes from studies of brain-damaged patients (Gazzaniga & Smylie, 1983; Milner & Taylor, 1972; Riege, Metter, & Hanson, 1980; Whitehouse, 1981). These studies suggest that verbal and nonverbal codes may be processed in different hemispheres. For example, "split-brain" patients – epileptic individuals who have had communication between their cerebral hemispheres disrupted to minimize the spread of seizure activity – perform significantly better on tests of face memorization when faces are presented to the right hemisphere than the left hemisphere (Gazzaniga & Smylie, 1983), indicating that the right hemisphere may have an advantage in processing nonverbal materials.

Recent brain imaging studies have demonstrated that memorization of materials associated with different codes can activate distinct regions of left and right frontal cortex. As discussed above, encoding of verbal material such as words is associated with activation in specific left frontal regions. By contrast, memorization of unfamiliar faces (Kelley et al., 1998; McDermott, Buckner, Petersen, Kelley, & Sanders, 1999) and texture patterns (Wagner et al., 1998a), neither of which can be easily associated with a verbal label, additionally activates *right* frontal regions.

An intriguing interpretation of these findings is that distinct regions of frontal cortex will, for a single event, code multiple kinds of verbal and nonverbal information and facilitate memory performance. This interpretation is consistent with multiple-code models of memory (Paivio, 1986; Nelson, 1979) and provides another example of a psychological phenomenon mapping onto specific aspects of measurable brain function (but see Grady et al., 1995; Haxby et al., 1996).

Again, it is also important to note that the emphasis in this paper on frontal regions should not be taken to imply other brain regions are not important. For example, Nyberg et al. (1996b) have found evidence that parietal and occipital–temporal regions make specific contributions to different kinds of encoded information. Additionally, Wheeler, Petersen, and Buckner (2000) found that certain regions of visual and auditory cortex were activated during perception and recall of picture and sound information, indicating that these regions are involved in initial encoding as well as subsequent retrieval processes (see also Zatorre, Halpern, Perry, Meyer, & Evans, 1996; Nyberg, Habib, McIntosh, & Tulving, in press). Frontal cortex likely contributes, in concert with other brain regions, to the processes by which information is eventually bound into code-specific components of an episodic memory. A task for the future will be to more precisely characterize the behavior and function of the distributed networks that contribute to episodic encoding processes.

3. Episodic encoding is a by-product of on-line processing within the frontal cortex

The data reviewed above tentatively suggest a simple idea – perhaps what might even be considered a theory – of how an episodic memory is formed. Under normal circumstances, *an episodic memory is formed when information is elaborated upon via specific frontal regions and the memory will contain distinct code-specific components depending upon which specific frontal regions participate*. It is notable that the frontal regions whose activity correlates consistently with episodic memory formation are also associated with verbal working memory and word generation tasks (tasks requiring elaboration and manipulation of verbal representations). These activity correlates may be part of the neural substrate that maintains representations on-line (in working memory) while the representations are manipulated and used to guide and/or select further on-line events. At the same time however, these representations may themselves be involved in encoding episodic memories. By this account, the encoding is essentially a by-product or secondary effect of on-line processing.

This theory is appealing because it can account for a number of behavioral influences on episodic memory formation by relating them to functional changes in brain activity. For example, it provides an explanation of the "levels or processing" effect at a functional–anatomic level (Craik & Lockhart, 1972; Craik & Tulving, 1975). Processing that requires verbal elaboration (deep processing) appears to activate specific regions of left frontal cortex, including ventral regions near BA 44/45/47, whereas well-automated language tasks and those based only on phonological processing (shallow tasks) do not. Shallow encoding tasks may not encourage the formation of episodic memories because they do not require representation of information in these ventral prefrontal regions.

There is one question which must be addressed in relation to how frontal cortex participates in encoding; namely, exactly how does activity within frontal cortex interact with the medial temporal cortex to support encoding? This question is important, because the medial temporal lobes are known to be necessary for successful encoding. Damage to the medial temporal lobes, such as that observed in the amnesic patient HM (Scoville & Milner, 1957), is often associated with partial or near complete loss of the ability to remember new experiences (including episodic memories) in the presence of relatively intact cognitive functioning in other domains (see, Cohen & Eichenbaun, 1993; Corkin, 1984; Squire, 1987). Non-human primate models of memory loss also suggest that lesions within hippocampus and adjacent cortex (within the medial temporal lobes) result in an impaired ability to remember new experiences (Murray, 1996; Zola-Morgan & Squire, 1993). These data strongly suggest that medial temporal lobe regions play a critical role in memory formation.

Nonetheless, according to the ideas presented here, episodic memory formation of deeply or elaborately processed information involves participation of both frontal and medial temporal regions. Specifically, we hypothesize that frontal cortex provides a source of information (an input) to medial temporal lobe structures during encoding (Buckner, 1999; Buckner et al., 1999; Moscovitch, 1992). Such a notion fits well with proposal that medial temporal lobe structures (including the hippocampus and adjacent structures) play a role in binding – or the integration and cohesion of incoming information – to form lasting memories (Cohen & Eichenbaun, 1993; Moscovitch, 1994; Johnson & Chalfonte, 1994; McClelland, McNaughton, & O'Reilly, 1995; Schacter, Norman, & Koutstaal, 1998). The emphasis of the present paper, however, is that frontal cortex provides a critical input to these medial temporal structures supplying the necessary "ingredients" that must be bound together to form an episodic memory. Thus, both frontal and medial temporal regions will be critical to the conception of an episodic memory – and the lack of participation of either brain region will disrupt episodic memory formation.

The idea of frontal modulation of medial temporal cortex is not new. For example, Moscovitch (1994) suggests that the frontal lobes "are prototypical organization structures crucial for selecting and implementing encoding strategies that organize the input to the hippocampal component" (p.278). Similarly, Squire (1987) suggests that "Frontal cortex presumably performs its computations on many kinds of information, which are analyzed concurrently for other purposes by other regions of cortex. Frontal cortex allows information to be remembered in its appropriate context, that is, in the correct temporal coincident event. The medial temporal region then operates upon this information, allowing it to endure in the organized form it has achieved in neocortex" (p.239). We reemphasize this view here in the context of newer brain imaging studies.

Further bolstering the case for frontal–medial temporal interactions in episodic memory formation, it can be shown that if one region is intact and functioning in *other* tasks, but the other region is damaged, the formation of episodic memories is imparied. For example, lesions to the medial temporal lobes leave frontally mediated processing undisturbed. In particular, patients with medial temporal lobe damage can clearly perform well on many tasks that demand meaning-based elaboration – processing that depends on frontal activity and which would normally contribute to episodic memory encoding. Nonetheless, in the presence of medial–temporal lobe damage, frontally mediated processing will not lead to episodic encoding.

A study in which an amnesic subject was imaged using fMRI illustrates this point. Buckner and Koutstaal (1998) studied Patient PS – a 46 year old woman who suffered severe amnesia following a period of anoxia many years earlier. Structural MRI revealed a lesion that included portions of the medial temporal lobes. PS was imaged using fMRI during a meaning-based (deep) word judgement task and showed clear activation of frontal regions, similar to that found in normal individuals performing the task. Nonetheless, following the fMRI imaging session, patient PS was unable to remember any words, or even whether words or pictures had been presented. For patient PS, frontally mediated processing did not lead to episodic memory formation, probably due to her medial temporal damage.

Correspondingly, as evidenced by the numerous brain imaging studies referenced above, normal subjects with intact medial temporal lobes fail to form memories when frontal activity is not present. It is further important to note that frontal lesions produce episodic memory impairments, just not selectively so (e.g., Wheeler, Stuss, & Tulving, 1995; Shimamura, Janowsky, & Squire, 1991; Schacter, 1987). This is likely because, unlike medial temporal lobe contributions to episodic memory formation, frontal contributions arise as a secondary effect of their engagement to complete on-line task goals. If frontal activity plays both an immediate task-related role, and a secondary role in providing an input to the medial temporal lobes, there may be inherent difficulties in trying to associate memory function with frontal injury. Lesions to frontal regions will produce speech and verbal fluency impairments if the lesion is in left frontal cortex (Geschwind, 1979) and visuospatial impairments if the lesion is localized to right frontal cortex (Corballis et al., 1999), consistent with the role of frontal cortex in on-line processing associated with these functions.

Nonetheless, frontal lesions may also have important, but sometimes overlooked, effects on episodic memory encoding (Buckner & Tulving, 1995). Consistent with this idea, patients with speech and fluency difficulties typical of left frontal damage do poorly on recognition tests of studied words (Riege et al., 1980; Whitehouse, 1981). These studies also included patients with deficits likely arising from damage to similar frontal regions in the right hemisphere. Consistent with the findings discussed above concerning multiple-code models of human memory, these patients were impaired at remembering nonverbal items, including pictures (Riege et al., 1980; Whitehouse, 1981) and birdsongs (Riege et al., 1980).

The findings reviewed above further suggest a unidirectional flow of information from frontal to medial temporal regions during encoding. Perhaps the strongest evidence for this unidirectional hypothesis comes from patient data; namely the finding that medial temporal lesions do not produce on-line processing deficits that would be associated with frontal lesions. In addition, the brain imaging data from the amnesic subjects tentatively suggest that normal frontal activity will occur in the presence of medial temporal damage. Perhaps, in these patients, functioning frontal regions may be sending information to silent brain areas critical for later stages of memory formation.

However, in the context of normal cognitive operations it seems possible that frontal and medial temporal regions influence each other, especially when possible roles of these structures in memory retrieval (e.g., Schacter et al., 1998) or novelty detection (Tulving et al., 1994) are considered. That is, the products of medial temporal processing likely influence frontal cortical processing. We do not discuss retrieval or novelty detection in detail because they are outside the scope of the present article; the focus here relates only to the initial encoding of an event. Nonetheless, we highlight the possibility of bi-directional information flow between frontal and medial temporal regions. Testing between and/or tying together these varied perspectives is an important topic for future investigation.

4. Conclusion

In conclusion the findings and interpretations presented here expand on general ideas about the importance of frontal and medial temporal regions in memory. We draw from recent functional brain imaging studies of memory encoding to suggest that the frontal cortex provides an essential input to medial temporal regions during the formation of an episodic memory. Importantly, the specific regions of frontal cortex that are active appear to be dependent upon current task goals and the on-line processing that results. Consequently, different regions of frontal cortex are active when verbal and nonverbal stimuli are presented, and when different types of verbal processing (e.g., phonological versus semantic) are encouraged. In each case, however, the processing is hypothesized to provide a critical input to the medial temporal lobes, contributing to the lasting formation of an episodic memory. Of course the ideas presented here are simply meant as heuristics which highlight a small but important subset of the functional anatomy underlying episodic memory formation. Frontal cortex activity and interactions with medial temporal lobe structures are undoubtedly not the only determinants of memory formation, but their presence appears to be key element of episodic encoding and worthy of further study.

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