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Observing the transformation of experience into memory

Ken A. Paller and Anthony D. Wagner

The ability to remember one's past depends on neural processing set in motion at the moment each event is experienced. Memory formation can be observed by segregating neural responses according to whether or not each event is recalled or recognized on a subsequent memory test. Subsequent memory analyses have been performed with various neural measures, including brain potentials extracted from intracranial and extracranial electroencephalographic recordings, and hemodynamic responses from functional magnetic resonance imaging. Neural responses can predict which events, and which aspects of those events, will be subsequently remembered or forgotten, thereby elucidating the neurocognitive processes that establish durable episodic memories.

Some of life's episodes are remembered so well that we can accurately bring back to mind or recollect tremendous detail, even after considerable time has elapsed. Other events are seemingly experienced in an identical way, and yet are irretrievably lost from memory, even moments later. A fundamental challenge for memory theorists is to specify the neurocognitive processes that impact the mnemonic fate of our experiences, influencing whether they will be remembered or forgotten. A significant step towards meeting this challenge is to delineate encoding operations and their impact on subsequent memorability. Although multiple factors influence our ability to remember, one factor that must be critical for remembering is whether the experience coincides with the effective laying down of an engram in the brain. Insights into effective memory formation can be gained by monitoring brain activity during an experience and relating these neural measures to behavioral evidence that a memory was formed. In this review, we consider how correlations between neural activation and subsequent remembering have informed our theories of how experiences are transformed into memories.

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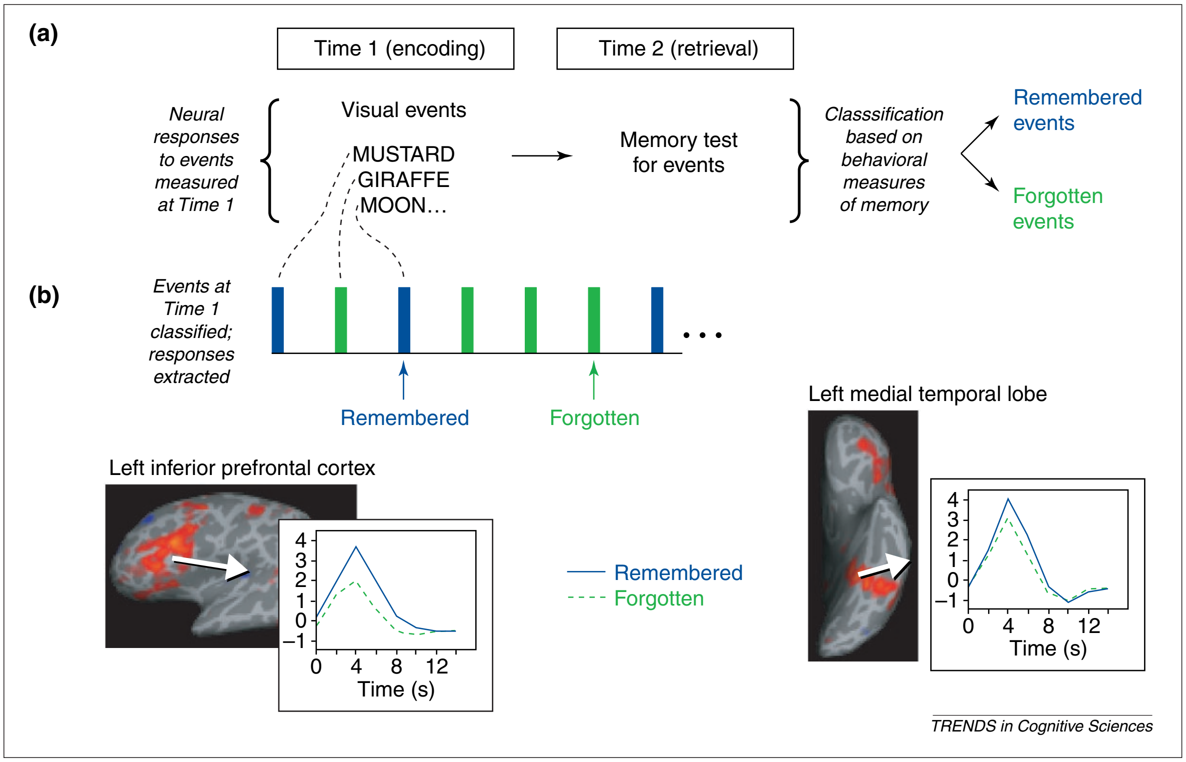

Fig. 1. The subsequent memory paradigm. (a) Neural responses are acquired during event processing (in this example, visual word presentations). Subsequently, memory is probed and events are classified. (b) Neural responses are analyzed based on subsequent memory, revealing neural correlates of encoding in various brain regions. Graphs (redrawn from Ref. 8) show that remembered events (blue) elicited greater responses than forgotten events (green).

The first steps to remembering: witnessing the creation of memories

Episodic encoding refers to the initial information processing steps whereby a memory trace is created such that it can subsequently support the conscious recollection of one's past [1]. Encoding depends on at least two components:

(1) The initial component mediates the transformation of sensory input into internal representations that are interpreted or comprehended. This often entails the retrieval of associated knowledge relevant to current goals.

(2) The second component binds the internal representations into an enduring trace such that the resultant representation ultimately permits the experience to be brought back to mind. The representation may include perceptual and conceptual fragments, self-generated thoughts, and contextual details, and critically links such fragments together to form an integrated engram.

These two components of encoding are clearly illustrated by patterns of spared and impaired performance in individuals with anterograde amnesia due to bilateral medial temporal or diencephalic insult. Patients with amnesia can carry on a normal conversation, repeat back information when queried immediately after the information is provided, and show intact working memory [2]. Thus, they can generate and work with internal representations, but have difficulty remembering experiences once active representations have dropped from consciousness. Contemporary explanations for this pattern typically posit a deficit at the second stage of encoding, whereby durable relational, configural, or declarative traces are formed and/or consolidated [3–7].

The two components of intact episodic encoding – generating an internal representation of an experience and storing a bound trace of those representations – typically interact during learning. We describe below how these interactions may reflect the convergence of (1) prefrontal and posterior neocortical computations responsible for the representation and goal-directed processing of events with (2) medial temporal computations that guide the storage of durable episodic traces whereby the elements of these representations are linked together.

To learn how experiences are transformed into memories, no single methodology will suffice. Cognitive neuroscientists strive to obtain precise observations of both the behavior that arises from cognitive processes and the neural computations that support cognition. A particularly powerful approach to the study of memory encoding is the 'subsequent memory paradigm' (see Fig. 1), which provides measures of neural activity correlated with later remembering. In general, neural responses to distinct stimulus events are recorded and then classified based on testing the subject's memory for the stimuli at a later time. The key contrast is typically between neural responses to stimuli later remembered and to those later forgotten. *D*ifferential neural activity based on *m*emory, sometimes referred to as *Dm*,

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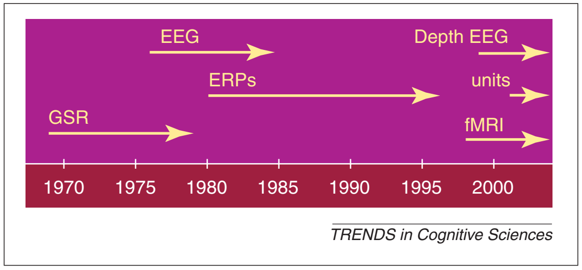


Fig. 2. Timeline of *Dm* analyses of episodic encoding. The current blossoming of interest in physiological correlates of memory encoding stems from earlier work using skin conductance measures (GSR). Measures of brain activity were subsequently used, including EEG measures in the frequency domain, event-related potentials recorded from scalp and intracranial electrodes, single unit activity, and functional magnetic resonance imaging.

provides an index of neural computations at the time of encoding that are predictive of accurate recall or recognition (Fig. 2). Subsequent memory effects, which presumably index pivotal operations at the time of learning that influence what will be remembered, constitute some of the tightest correlations between neural function and encoding. Here, we consider how the subsequent memory paradigm has shed new light on the complexity and variety of encoding processes, providing leverage on delineating how episodic memories are created.

Encoding circuits: evidence from stimulus effects

The cerebral cortex consists of multiple processing modules that represent and perform computations on specific stimulus dimensions or features, such as visual attributes, spatial configuration, and domains of meaning. High-level outputs from neocortical processing modules are directed to the medial aspect of the temporal lobe (MTL), which binds representations together in the service of episodic memory formation. Different combinations of neocortical circuits can thus potentially interact with the MTL; which specific circuits are recruited in any given instance of learning is a function of factors such as the nature of the event being encoded.

Accordingly, material-sensitive subsequent memory effects have been observed using ERPs and fMRI. For example, different brain potentials were correlated with later memory depending on whether subjects learned words or faces [9]. The two initial fMRI studies of subsequent memory effects [8,10] also revealed activation patterns that varied depending on the stimuli. Wagner and colleagues [8], as well as others [11–17], reported that subsequent recognition memory for incidentally learned words was correlated with greater encoding activity primarily in left inferior prefrontal cortex (PFC), fusiform cortex, and MTL. Topographic patterns of subsequent memory effects in scalp ERPs derived from current source density analyses have likewise been interpreted as reflections of left inferior PFC activity [18]. By contrast, Brewer and colleagues [10] observed that activity levels in bilateral MTL and right inferior PFC predicted subsequent remembering for incidentally learned complex visual scenes. Thus, verbal encoding was associated with left inferior PFC and MTL computations, and pictorial encoding with right inferior PFC and bilateral MTL processing.

In a study that directly compared word and visual scene encoding, contrasts between novel and highly familiar stimuli were juxtaposed to subsequent memory effects [12]. Scene novelty preferentially activated right inferior PFC and bilateral posterior fusiform, consistent with their putative role in processing visuo-spatial/visuo-object information [19,20]. Word novelty preferentially activated the posterior extent of left inferior PFC and left anterior fusiform, perhaps reflecting phonological and/or lexical computations. Word novelty also selectively activated the anterior extent of left inferior PFC and left middle/inferior temporal cortex, regions involved in the representation and controlled retrieval of semantic knowledge [21]. Speculatively, PFC regions may influence encoding by modulating posterior neocortical processing and by regulating input to MTL. Importantly, activity levels in almost all of these regions – as well as in MTL structures – were positively correlated with subsequent recognition memory for the novel stimuli. Thus, some cortical regions that are sensitive to stimulus novelty also support episodic encoding.

Emotional intensity is another stimulus-bound dimension that impacts encoding. Consistent with the hypothesis that the amygdala modulates episodic memory for emotional experiences [22,23], several groups observed between-subject correlations between subsequent episodic memory and levels of amygdala activation during encoding of blocks of negative and, in some studies, positive stimuli [24–26]. Within-subject fMRI analyses revealed that amygdala activation during the viewing of scenes was predictive of subsequent memory only for emotionally arousing scenes [27]. This approach illustrates the usefulness of combining behavioral measures (judgments of emotional arousal and subsequent memory) with indices of neural computation.

Processing goals influence encoding

The configuration of neocortical modules that mediate encoding varies not only with the nature of the stimulus but also with how attention is allocated to different stimulus features and types of processing. A central theoretical focus in memory research has concerned the influence of goal-directed attentional orientation on encoding, as can be manipulated by instructions to process stimuli for meaning, phonology, or structural form [28,29]. Initial PET and fMRI studies of encoding using blocked designs exploited the superiority of meaning-based versus non-semantic orientation to show, for example, that specific left PFC networks are involved in semantic encoding (for a review see Ref. [30]).

The influence of attentional orientation on *Dm* has also been explored with event-related designs. In one study, for example, ERPs were examined for words studied under four different attentional orienting conditions, using two structural and two semantic tasks [31]. *Dm* effects – enhanced posterior positivity at a latency of 400–800 ms for subsequently remembered words – were greater during semantic than during non-semantic orienting. These findings, along with other ERP evidence [32–37], suggest that some *Dm* effects reflect processing variations that come into play chiefly when subjects maintain a meaning-based attentional orientation, and that different meaning-based goals can differentially influence encoding. As a general rule, *Dm* can emerge when the type or degree of processing varies from trial to trial so as to produce subsets of strongly and weakly encoded items, and when that processing is sufficiently time-locked to stimulus presentation.

In recent fMRI studies, incidental learning paradigms were used to determine whether different encoding networks were engaged during semantic versus non-semantic processing. For words processed in a semantic manner, activation based on subsequent recognition was observed in left inferior PFC, fusiform, MTL, and right inferior PFC [13,14,16]. For words processed in a structural manner, in two studies the subsequent memory effects were observed in a subset of these regions; namely, left inferior PFC and anterior MTL [13] or left PFC, fusiform, and right PFC regions [14]. In both studies, no additional regions differentially predicted subsequent memory following non-semantic orienting (but see Ref. [36] for divergent ERP results), suggesting that the frontal-temporal encoding circuit recruited during non-semantic orienting may be a subset of the circuit recruited during semantic orienting.

Failure to observe *Dm* effects that are greater following non-semantic, relative to semantic, orienting may be partially attributable to low power due to poor later remembering following structural encoding [16,31] as well as to the obligatory nature of phonological and structural processing during semantic orienting. However, prior observations of crossover semantic/phonological interactions within left PFC, posterior temporal and parietal cortices [38], raise the possibility that semantic and non-semantic *Dm* effects sometimes diverge. Indeed, new evidence along these lines was recently obtained by comparing semantic to phonological conditions [16]. Whereas activation in left and medial PFC regions predicted recognition following semantic orienting, activation in bilateral intraparietal, fusiform, right PFC, and left occipital regions predicted recognition following phonological orienting. The specific PFC-posterior neocortical circuits that subserve encoding partially depend on the event features attended during learning, either due to differences in the stimulus-bound features or in the individual's attentional goals. Encoding emerges as a byproduct of such goal-directed event processing [8,16,28].

The allocation of attention can be directed not only to a single stimulus but also to associative processes whereby two or more stimulus items are processed in relation to one another (i.e. *inter*-item rather than *intra*-item processing [39]). In one ERP study, recognition was superior for associatively compared to nonassociatively encoded word pairs, and *Dm* was observed only for the associatively encoded pairs [40] (see also [41] for a contrast between different types of associations). By contrast, an fMRI study of intra-item (rote) and inter-item (elaborative) rehearsal of three simultaneously presented words revealed subsequent memory effects primarily following rote rehearsal, although a *Dm* effect in left hippocampus was specifically associated with item recognition following elaborative encoding [17]. Associative or elaborative inter-item processing, which probably demands strategic rehearsal and manipulations of actively maintained representations [42], may likewise underlie frontal *Dm* findings in ERP studies when subjects processed relations between individual items [43,44].

Fractionating episodic memory

The experience of an episode does not yield a single, undifferentiated memory trace. Rather, multiple forms of learning simultaneously occur during event processing. Subsequently, those various traces can support qualitatively different memory phenomena. For instance, behavioral and neuropsychological evidence suggests that memory for the prior occurrence of a stimulus is distinct from memory for a conglomeration of specific details about that prior experience. In the latter case, the retrieval of multiple associations between a stimulus and contextual cues tends to coincide with recollection, the subjective experience of remembering. Item-context associations can pinpoint the source of remembered information, and thus drive the full-blown recollection of an episode [45]. On the other hand, a stimulus can also be recognized in the absence of recollection. In this case, retrieval may support a phenomenon known as 'familiarity without recollection' [39,46].

The specific neurocognitive processes that support these two manifestations of episodic memory, recollection and familiarity, have been investigated intensely but remain under active debate [47–49]. One hypothesis is that parahippocampal/perirhinal computations contribute mainly to memory for the occurrence of an item, which can underlie subsequent recognition based on familiarity [50,51]. The hippocampus, in contrast, may mediate or participate in the encoding of relations or conjunctions between an item and its context as well as conjunctions between items, which are crucial for subsequent recall and recollection-based recognition [3,7,52,53].

Memory testing with the 'R/K procedure' has been used to distinguish between recollection and familiarity-without-recollection by requiring people to indicate their basis for recognition, either 'remembered' (R) or 'known' (K) [54,55]. Several ERP studies have combined R/K judgments with *Dm* analyses [35,44,56]. For example, larger positive responses were observed for subsequently recollected items than either known items or items not recognized, with no ERP differences between the latter two conditions [35]. These ERPs associated with subsequent recollection may fall into the broader category of the parietal-maximum *Dm* observed by many investigators and generally more robust with recall than with recognition [37,57,58]. On the other hand, in one study an ERP correlate of encoding supporting familiarity was ascribed to an N340 potential thought to be associated with attention-dependent conceptual processing in left temporal and/or inferior frontal neocortex [44].

The reliability of *Dm* analyses can generally be enhanced when recollective experience or decision confidence is taken into account. Subjects with a preponderance of correct guesses, with lenient criteria for judging items to be old, or with criteria that vary erratically over the course on an experiment, may not show *Dm* effects. Consistent with this suggestion, reliable *Dm* effects can be apparent in fMRI studies particularly when confidence or R/K judgments were required during recognition. These procedures restrict analyses to the memory extremes, consequently minimizing the influence of guessing. Accordingly, fMRI *Dm* magnitudes tend to be larger for events later recognized with high relative to with low confidence [8,13] and also larger for events later 'remembered' than during those later 'known' [10,11].

To date, fMRI studies have not provided clear evidence for a qualitative difference between encoding that yields recollection versus familiarity alone. Brewer and colleagues [10] observed graded encoding activation that declined across subsequent remembering to knowing to forgetting, suggesting merely quantitative differences. Henson and colleagues [11] did not run conventional subsequent memory analyses because of low levels of forgetting, but did compare encoding activations as a function of whether recognition was associated with an R or K response; activation in left inferior and middle PFC and left precuneus was predictive of 'remembering,' whereas activation in right parahippocampal gyrus and precuneus was predictive of 'knowing.' Additional evidence from studies that explore the relation between *Dm* for subsequent source recollection and for item memory without recollection, relative to forgotten trials, may prove informative in clarifying whether different encoding processes promote memory with and without recollection.

An intriguing speculation regarding the relation between ERP and fMRI results, made by Friedman and Johnson [18], is that parietal scalp ERP subsequent memory effects could derive from left precuneus computations associated with encoding [11]. Of course, combining ERP and fMRI data to achieve high temporal and high spatial resolution will ultimately require additional evidence that the same neural activity is responsible for both effects. Nevertheless, this possible multimodal imaging integration highlights the potential fruitfulness of such efforts. Relative timing data that show when encoding-related processes are set into motion can be used together with localization data from neuroimaging to provide new insights into the cognitive functions of specific neural computations.

Although familiarity entails episodic memory restricted to a single item, it must be distinguished from another sort of item-specific long-term memory known as priming. Is this non-conscious facilitation or biasing of stimulus processing due to recent experience supported by the same encoding events that support episodic encoding? In two attempts to address this question, ERPs were found to predict subsequent recall and recognition but not priming [59,60]. However, it has recently been suggested [35] that when intentional encoding is avoided, ERPs can predict subsequent priming [35,61]. A critical issue for future investigation is thus to characterize the relation between processes supporting priming and those yielding effective episodic memory.

Indeed, priming can act to hinder episodic encoding under some circumstances. Wagner and colleagues [62] found that the magnitude of priming during word processing was inversely related to episodic learning, as indexed by subsequent recognition. Priming was manipulated by interposing either a long or short lag between initial and repeat trials. Neural priming in left inferior PFC was greater with the short lag, as was behavioral priming. Subsequent recognition was superior with the long lag, the condition yielding less priming. Between-subject negative correlations were also observed between priming and subsequent recognition, even when lag was held constant. Priming might promote a stereotyped or sparse re-encoding experience, thus producing a less effective episodic memory [62].

Medial temporal contributions to encoding

Neocortical and medial temporal regions make different contributions to episodic memory. Even with a severe amnesia, the active representation of the multidimensional features of moment-to-moment experiences can still be supported by neocortical mechanisms. By contrast, *storing* neocortical memory fragments as coherent episodic representations is characteristically problematic in amnesia. The hippocampus and associated MTL structures (perirhinal, entorhinal and parahippocampal cortices) might play an essential role in linking up the multiple representations, dispersed across distinct neocortical regions, that constitute an experience [3,6]. Consistent with this idea, MTL activation has been observed in blocked-design PET and fMRI studies of episodic encoding with item-based, associative, and novelty-assessment paradigms (for reviews see Refs [63,64]). But many questions remain regarding exactly how MTL-neocortical interactions support learning, when MTL computations are engaged, and whether distinct anatomical subregions within the MTL subserve distinct mnemonic functions.

ERP recordings from intracranial electrodes suggest that a posterior hippocampal contribution might begin within the first 300–900 ms after stimulus onset [65]. Color patterns that patients were required to remember in a delayed matching-to-sample test elicited larger hippocampal potentials than did similar stimuli presented during the delay or when recognition decisions were made. These potentials could reflect the recruitment of hippocampal circuitry during intentional encoding, although the small number of recognition errors prohibited an analysis to determine whether these potentials predicted subsequent remembering.

In other experiments using intracranial ERPs, subsequent memory analyses were used to implicate specific MTL structures in encoding. Within-subject *Dm* effects were found for visual words based on recall after a filled 30-s delay [66,67]. Potentials that reached a negative peak 400–500 ms after word onset were larger for subsequently recalled words. These potentials, putatively generated in rhinal cortex (i.e. entorhinal and perirhinal cortex, the site of principal connections between hippocampus and neocortex), were thought to reflect the richness of semantic analysis [67]. By contrast, hippocampal *Dm* effects, which arose only after the rhinal potential peak, were thought to reflect trial-by-trial differences in associative learning processes that can begin only after initial semantic analyses.

Single-unit recordings from the human hippocampus further indicate that the rate of neural firing in this structure varies with encoding [68]. In response to visual presentations of to-be-remembered word pairs, firing rates of some neurons demonstrated a positive correlation and others a negative correlation with later cued recall.

MTL correlates of subsequent memory have also been demonstrated in several event-related fMRI studies. Encoding of words subsequently recognized was associated with activation in left posterior parahippocampal cortex [8,12] and left hippocampus [12,13,17]. Recall performance combined for groups of five words revealed correlated activity in posterior hippocampus [69] and tonic state effects in entorhinal cortex [70]. Subsequent recognition of complex visual scenes was correlated with bilateral posterior parahippocampal activation [10,12] and bilateral hippocampal activation [12].

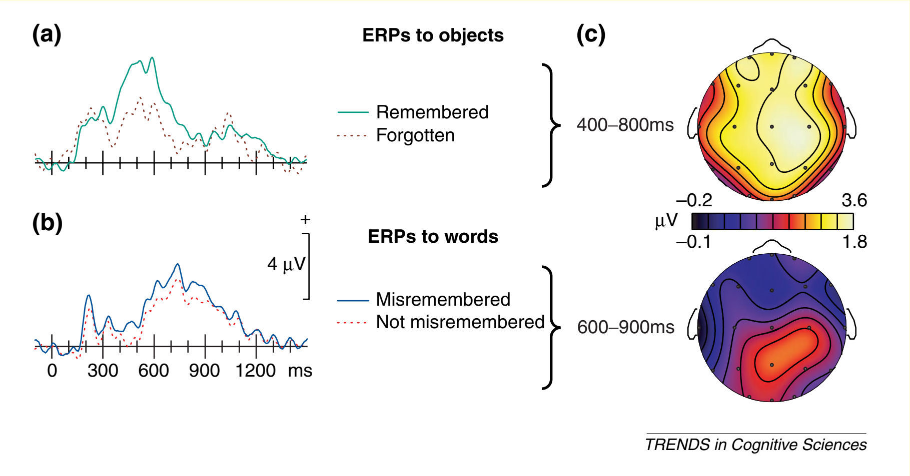
The MTL regions implicated in these fMRI studies – typically posterior parahippocampal cortices and hippocampus – were not always the same as those observed in intracranial ERP experiments. Such discrepancies could potentially result from: (1) differences in the cognitive paradigms implemented; (2) the fact that ERPs and fMRI may detect different subsets of neural activity; (3) limits on fMRI sensitivity in anterior MTL; (4) limited intracranial ERP sampling from MTL regions; or (5) pathology or medication effects in patients with intracranial electrodes. Importantly, Strange and colleagues [71] reported subsequent memory effects in perirhinal, hippocampal, and posterior parahippocampal regions when they adopted the same cognitive paradigm as in prior intracranial ERP experiments [66] and optimized the fMRI scanning protocol for sensitivity to anterior MTL signals. A complex pattern of functional dissociations was observed across MTL subregions based on serial position within the learning list [71]. Further clarification of possible functional subdivisions within the MTL might be gained through subsequent memory analyses for contextual information or for associations between the constituent elements of an episode.

In a novel investigation of MTL regions and their interactions during encoding, the subsequent memory methodology was applied to single-trial EEG in the gamma frequency range (32–48 Hz) [72]. An increase in phase synchronization between rhinal and hippocampal regions (100–300 ms and 500–600 ms) followed by a decrease in synchronization (after 1000 ms) suggested that an initially enhanced interaction between processing in these two regions may reflect encoding computations that facilitate later recall. Changes in synchronization could emerge directly from the dynamics of the MTL circuit or as the result of an external signal that entrains the MTL circuit [72]. Given the repeated observation of PFC correlates of subsequent memory, one speculative source of top-down gating of the MTL might be PFC control processes [73]. Other EEG analyses in the frequency domain suggest that successful episodic encoding is associated with a scalp-recorded increase in theta power (as defined on an individualized basis, generally in the 4.0–7.5 Hz range) [74,75]. Klimesch speculated that this theta activity is induced in neocortical regions via cortico-hippocampal feedback loops [76]. Scalp-recorded theta synchronization also has been used to implicate cooperative activity across neocortical regions during encoding [77].

The existing data suggest that episodic encoding processes are dependent upon MTL networks in conjunction with other neocortical networks. Yet,

Box 1. How the brain creates false memories

Memories are not always accurate. Encoding processes can sometimes support the subsequent recollection of a false memory. One type of false memory occurs when someone recalls an episode that was imagined and mistakenly believes that it had actually occurred. Gonsalves and Paller set up a laboratory experiment in which both accurate memories and false memories of this sort were produced [a]. Furthermore, different brain potentials at encoding were associated with accurate versus false memories. The accurate memories were for photos of objects viewed on a video monitor. ERPs to objects presented during the study phase differed as a function of whether the object was later remembered or forgotten on a subsequent recognition test, in which the names of those objects were spoken (Fig. Ia).



TRENDS in Cognitive Sciences

Fig. I. Brain potentials associated with the formation of true and false memories. (a) ERPs to objects were averaged according to whether those objects were subsequently remembered. (b) ERPs to words were averaged according to whether people later mistakenly thought they had seen the corresponding objects. Recordings were from the midline occipital scalp location. (c) Topographic maps were interpolated based on differences between pairs of waveforms at each electrode location (shown by small circles). (Adapted from Ref. a.)

Visual words were also presented during the study phase, and people were instructed to mentally generate a visual image in response to each word. ERPs to those words differed according to whether or not people subsequently claimed to have seen the corresponding object as a photo on the video monitor. (This contrasts with results from an experiment on another sort of false memory, memory conjunction errors, in which ERPs at encoding were not predictive of whether errors would occur at test [b].) As shown in Fig. Ib, ERPs from 600–900 ms were more positive for later false memories than when people later responded correctly that they had not seen that object. Similar ERPs recorded in a prior experiment had been associated with generating visual images in response to words [c].

The results from these two experiments taken together [a,c] support the following explanation for this type of false memory. The more vivid, detailed, or robust the visual imagery generated in response to a single word, the more likely the memory for that imagery will be mistakenly attributed to a memory resulting from actually viewing the corresponding object. Strong visual imagery at encoding promotes the retrieval of perceptual detail at test, which is generally a diagnostic sign of an episodic memory [d]. In some cases, however, such perceptual detail can be misleading and lead to a false memory, as when people claim to remember an event that was imagined but that never actually happened. The topographic maps (Fig. Ic) show that ERP differences associated with subsequent accurate memories were widespread across the scalp, whereas ERP differences associated with subsequent false memories were restricted to posterior scalp locations.

A recent fMRI study using the same paradigm showed that activation in a large set of brain regions, including prefrontal cortex, fusiform gyrus, and hippocampus/parahippocampal gyrus, predicted later accurate memories for objects, whereas activation in the precuneus, anterior cingulate and inferior occipital gyrus predicted later false memories [e]. An intriguing possibility is that the misleading visual imagery responsible for false memories in this paradigm was produced by neural networks in the precuneus, a region hypothesized to play a role in representing internal visual images [f].

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considerable controversy remains regarding the distinctive contributions that specific MTL subregions make. Moreover, the posited importance of PFC–MTL interactions remains to be empirically tested. Resolution of these fundamental questions should prove central to unraveling the mysteries of MTL contributions to memory formation.

Reverse engineering cognitive architecture

To what extent can episodic encoding be influenced by working memory maintenance processes? A prevalent view is that '"mindless" rote rehearsal *per se* is insufficient to create durable memories' ([78] p. 23). This view is based on the lack of a correlation between rehearsal duration and later recall [79,80], and the robust effects of levels-of-processing on episodic memory. However, behavioral evidence that rote rehearsal can facilitate subsequent recognition [81–83] has been substantiated by fMRI evidence that activation levels during rote rehearsal, in neural regions associated with phonological working memory, correlate with later recognition [17]. Given the minimal impact of rote rehearsal on free recall, it may be that phonological maintenance can support subsequent item recognition but not recollection.

Theorists have also examined the impact of retrieval processes on encoding. Retrieval is a particularly powerful incidental learning experience [84,85]. Encoded experiences that are later retrieved are subsequently better remembered compared to experiences not receiving retrieval practice [86]. Moreover, the magnitude of fMRI activation during recognition judgments on foils (unstudied words) was predictive of whether the foils were later recognized or forgotten [15]. The relation between engagement of retrieval circuits when accessing memories of studied items and later memory for those items remains to be determined.

Encoding/retrieval correlations point to a related question: How can certain processing produce forgetting? Retrieval of some memories results in the suppression [87] or blocking [88] of other, non-retrieved traces. Neuroimaging predictors of retrieval-induced forgetting could prove invaluable for understanding suppression and blocking. More generally, neural computations correlated with forgetting are beginning to garner attention: across four fMRI studies, forgetting was correlated with greater activation in dorsolateral and medial PFC, posterior cingulate, and parietal structures [8,89,90]. These ‘subsequent forgetting effects’ could reflect either (a) a diversion of neurocognitive resources away from processes that yield effective encoding, or (b) encoding processes that yield undifferentiated traces, leading to more interference.

Finally, it is worth noting that subsequent memory analyses can shed light on diverse cognitive and social-cognitive phenomena. For example, studies have explored the relations between encoding and later false remembering (Box 1) and between perceptual expertise and the phenomenon that people remember faces of their own race better than those of other races [91].

Conclusion

The ability to remember an episode is a function of multiple processes, some of which are engaged at encoding, some at retrieval, some in-between, and some emerging as an outcome of how encoding and retrieval processes interrelate. Intermediate processes constituting additional encoding or consolidation may be particularly critical for the stability of episodic memories over time [92–94]. One limitation of current implementations of the subsequent memory paradigm is that such intermediate processes are seldom indexed. Here, we focused on the initial processing of event information to illustrate the wealth of evidence available, and potentially obtainable, based on analyses of neural correlates of encoding.

Although subsequent memory analyses by themselves do not conclusively demonstrate causality with respect to encoding, transcranial magnetic stimulation when applied to fMRI-identified structures could serve as a critical test of the necessity of specific neural computations for learning. Whereas subsequent memory analyses can be central to investigations of episodic encoding, this approach is most informative when combined with a full range of complementary approaches (see Box 2). Identifying the relevant neural events in this way does not merely reveal where encoding happens, but rather serves to clarify how multiple processes optimally coalesce such that we can successfully remember the past.

Box 2. Observing mind and brain to track episodic encoding

(1) Brain imaging during direct manipulations of encoding

- Acquisition versus retrieval
- Levels of processing (e.g. deep vs shallow)
- Intention to remember
- Novelty

(2) Post-hoc item-by-item, state, and between-subject analyses

- Comparisons based on subsequent remembering or forgetting of items (*Dm* effects)
- Subsequent memory analyses emphasizing specific aspects of episodic memories (e.g. source, familiarity)
- Analyses of state changes that influence encoding (e.g. slow and sustained changes in attention or arousal)
- Between-subject correlations between memory performance and the magnitude of neural responses

(3) Lesion and disruption approaches

- Analyses of encoding in patients with memory disorders
- Temporary neural disruption (e.g. electrical or magnetic stimulation)

(4) Integrated methods

- Juxtaposing subsequent memory analyses with encoding manipulations
- Testing the causal role of subsequent memory effects via neural disruption
- Integrating electromagnetic and hemodynamic signals

Questions for future research

- Are the neural computations correlated with subsequent memory *necessary* for effective memory formation? Can they be selectively disrupted via transcranial magnetic stimulation such that forgetting results?
- How do global changes in cognitive set or attentional state, which remain undetected by typical subsequent memory analyses conducted at the item-level, impact encoding? How do the effects of global state interact with event-related encoding processes?
- How do prefrontal and posterior neocortical networks represent the diverse aspects of experience that form the building blocks of episodic memories? How do interactions between these brain networks and medial temporal networks support memory storage that can last a lifetime?
- What are the experiential prerequisites for episodic encoding? Can unconscious perception give rise to episodic memory for an event that was not consciously experienced?
- How do prefrontal control processes help to initiate the cascade of neural events that modulate encoding efficacy? Does this cascade begin with top-down prefrontal modulations, bottom-up posterior neocortical processes, or interactions of the two?
- How do the interactions that begin at encoding evolve over time, both across the course of an event as well as when consolidation and intervening retrieval events come into play? How do those intervening events regulate episodic forgetting?
- How does encoding differ for episodes versus other types of information such as facts, skills, and implicitly conditioned associations? Do the neocortical encoding events that putatively support priming constitute a subset of those supporting episodic learning or are they distinct?

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