Dissociable Spectral Components of Episodic Memory

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Abstract

Spectral analyses of electroencephalographic recordings have revealed frequency-specific power modulations that predict successful episodic memory performance. We argue that this literature implicates a spectral $T^{+}A^{-}G^{+}$ of mnemonic success, with increased low-theta (3-5 Hz), decreased alpha (8-12 Hz), and increased gamma (above 30 Hz) signaling successful encoding and retrieval across a broad range of memory tasks. We propose a component theory of $T^{+}A^{-}G^{+}$ in which low-theta and theta-coupled gamma support item-context binding, broadband gamma reflects effortful neural processing, and alpha suppression marks the engagement of a task-general effector mechanism. Although no single component is unique to episodic memory, their joint occurrence may be more selective for memory processes than any one alone.

Keywords: episodic memory, EEG, attention, cognitive neuroscience, neural oscillations

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Spectral signatures of memory

Early investigations into the electrical fields of the human brain revealed rhythmic activity which distinguished between wakeful rest and sleep [1]. Throughout the following decades, researchers sought to characterize this activity and its associations with various cognitive processes including motor planning [2] and perceptual processing [3]. To our knowledge, the earliest EEG study to directly examine memory processes in humans was published by Thompson & Obrist in 1964 [4]. Based on their analysis of scalp EEG recorded as participants either rested or learned sequences of nonsense syllables, the authors reported that learning was accompanied by reduced **alpha** activity (8–12 Hz; see Glossary) and increased “superimposed” waves, likely reflecting faster **gamma**-band activity (30–100 Hz).

Later studies developed the *subsequent memory* paradigm, which compares encoding-related brain activity for subsequently remembered and forgotten study items (Fig. 1). Differences between these conditions are called subsequent memory effects (**SMEs**). This approach, first applied using event-related potentials [5], later revealed a distinct pattern of spectral activity associated with successful encoding, characterized by increased low-**theta** (3-5 Hz; T^+), decreased alpha (A^-) and increased gamma (G^+). This pattern, henceforth referred to as $\mathbf{T^+A^-G^+}$, has been observed across a wide range of episodic memory tasks [6–10] (Fig. 2).

Despite its prevalence across many different studies and paradigms, the neurocognitive processes involved in $T^+A^-G^+$ have yet to be fully characterized. A central question is whether this pattern captures a single mechanism spanning across frequencies, or instead reflects multiple dissociable processes which independently contribute to mnemonic success. To address this, we will consider the spatial and temporal dynamics of $T^+A^-G^+$, and examine how it varies across experimental paradigms and individuals. If the effects emerge simultaneously across component frequencies, then this would indicate that

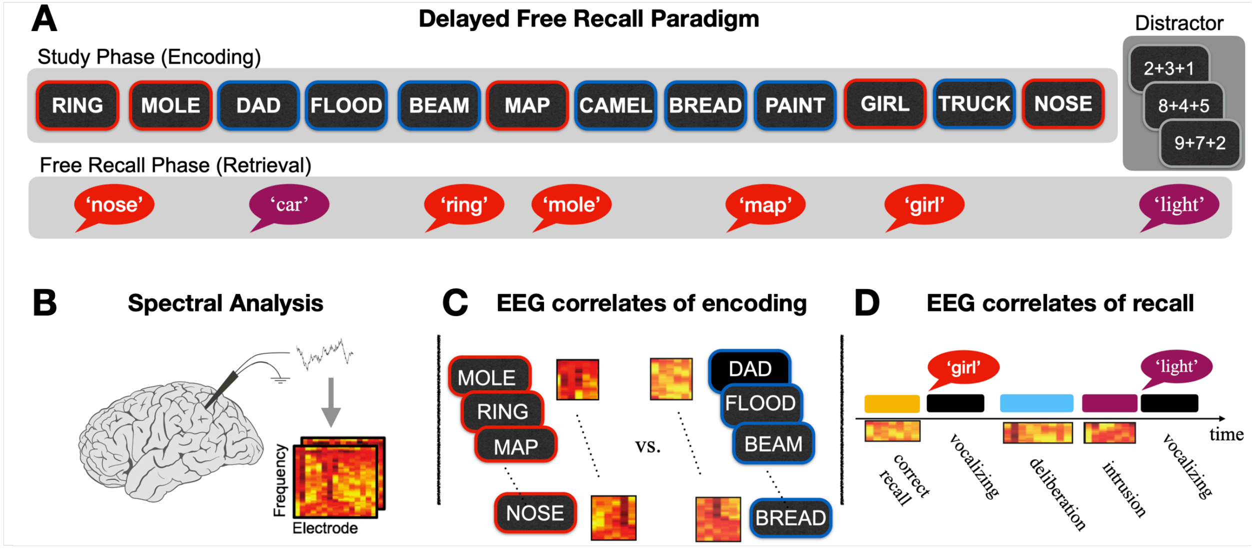


Figure 1. **Identifying neural correlates of successful memory encoding and spontaneous recall.** **(a)** Delayed recall: Subjects study individually presented items which they freely recall after a distractor-filled delay. **(b)** Each pair of electrodes generates a time series of field potentials. Applying spectral decomposition methods to a given interval produces a measure of power and phase at each frequency, illustrated across electrodes in the colored matrices. **(c)** Comparing brain activity during the encoding of subsequently recalled and non-recalled items identifies neural correlates of successful learning. **(d)** Comparing brain activity during the period immediately preceding spontaneous recall with matched periods of deliberation or memory errors (intrusions) identifies neural correlates of successful recollection.

$T^{+}A^{-}G^{+}$ reflects a single neural process which supports memory function. On the other hand, if the components can vary independently across time, spatial regions, individuals, and task demands, this would suggest that $T^{+}A^{-}G^{+}$ reflects the joint activation of multiple, distinct neural processes.

Also unclear is the degree to which $T^{+}A^{-}G^{+}$ is specific to memory. Does it capture the activation of a dedicated memory mechanism, or does it instead reflect generic factors such as task engagement and cortical arousal? We will evaluate this question by examining the consistency of $T^{+}A^{-}G^{+}$ across episodic memory processes, whether the pattern persists after controlling for cognitive effort or engagement, and whether it has been shown to generalize beyond episodic memory tasks.

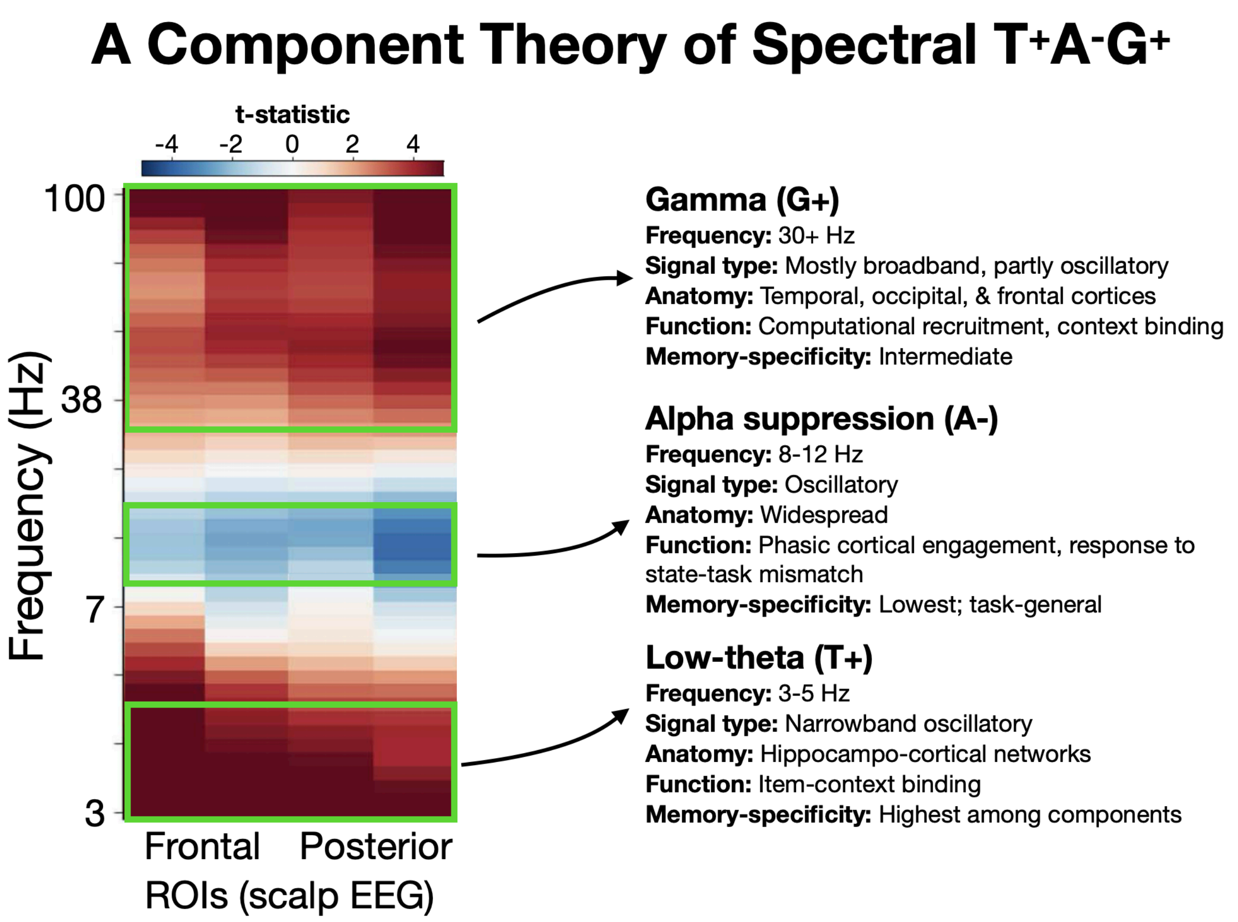
By reviewing the recent literature, we hope to clearly describe the conditions that lead to $T^{+}A^{-}G^{+}$ and what they reveal about its functional significance for memory processes. We will find that the evidence argues against the theory of a single mechanism of $T^{+}A^{-}G^{+}$, and that it likely reflects more than just cognitive effort or task engagement. We therefore theorize that $T^{+}A^{-}G^{+}$ captures the activation of multiple, dissociable neural processes that each play a role in supporting episodic memory function.

Box 1. Oscillatory vs. Broadband Theta

An extensive rodent literature implicates hippocampal theta as a key modulator of learning and memory, yet human hippocampal recordings have produced inconsistent results. Some intracranial studies report theta increases during successful encoding [8, 11], while others report decreases [12, 13]. In a review published in this journal, Herweg et al. [14] proposed three hypotheses to reconcile these findings. First, standard spectral methods confound narrowband **oscillatory** theta with broadband (**aperiodic**) power changes, such that broadband decreases during successful encoding could mask underlying oscillatory theta increases. Second, theta increases should be more visible in retrieval contrasts than in encoding contrasts, where broadband decreases more strongly obscure narrowband theta increases. Third, bipolar referencing may obscure theta increases by filtering out signals that are correlated across neighboring electrodes.

Rudoler et al. [15] evaluated all three hypotheses in hippocampal depth electrode recordings from 162 neurosurgical patients performing a free recall task. Using irregular resampling auto-spectral analysis (**IRASA**) to separate broadband and oscillatory activity, they found that broadband and narrowband theta exhibited opposite effects during encoding. Broadband power decreased for subsequently recalled items, while oscillatory theta increased. This memory-relevant signal was concentrated in the slow theta range (3-5 Hz), consistent with an extensive literature linking slow hippocampal theta to human memory [16–20], whereas faster theta (7–8 Hz) behaved more like alpha suppression. These findings are consistent with Herweg et al.'s first hypothesis that broadband averaging can obscure or reverse the positive oscillatory effect.

Rudoler et al. also found evidence supporting Herweg et al.'s second hypothesis. At retrieval, the positive low-theta effect was visible without IRASA correction, suggesting that broadband activity less strongly obscures the theta signal at retrieval than at encoding. This pattern was further supported by Herz et al. [21], who observed the full $\text{T}^{+}\text{A}^{-}\text{G}^{+}$ pattern in the hippocampus during correct recalls relative to intrusions and confirmed via IRASA that this pattern reflected genuine oscillatory activity. By contrast, Rudoler et al. did not find evidence to support the third hypothesis. Theta increases appeared similarly whether measured using bipolar referencing or whole-brain average referencing, indicating that referencing scheme alone does not account for the inconsistency in the literature.



A Component Theory of Spectral $T^+A^-G^+$

Gamma (G+)
Frequency: 30+ Hz
Signal type: Mostly broadband, partly oscillatory
Anatomy: Temporal, occipital, & frontal cortices
Function: Computational recruitment, context binding
Memory-specificity: Intermediate

Alpha suppression (A-)
Frequency: 8-12 Hz
Signal type: Oscillatory
Anatomy: Widespread
Function: Phasic cortical engagement, response to state-task mismatch
Memory-specificity: Lowest; task-general

Low-theta (T+)
Frequency: 3-5 Hz
Signal type: Narrowband oscillatory
Anatomy: Hippocampo-cortical networks
Function: Item-context binding
Memory-specificity: Highest among components

Figure 2. **Key figure: A spectral $T^+A^-G^+$ of episodic encoding and retrieval.** Schematic illustration of the $T^+A^-G^+$ pattern observed during successful episodic memory encoding and retrieval. Color mappings represent across-participant *t*-statistic comparing spectral power during recalled vs. nonrecalled trials (encoding) or pre-recall vs. deliberation (retrieval). Each frequency is annotated with its hypothesized signal type, neural source, and functional role within the component theory developed here.

$T^+A^-G^+$ across memory processes

If $T^+A^-G^+$ captures a meaningful neural signature of episodic memory, it should be observed across a range of memory paradigms and should generalize from encoding to retrieval. Here, we review the evidence for $T^+A^-G^+$ across these memory processes.

Encoding

The $T^+A^-G^+$ pattern predicts successful encoding across a broad range of episodic memory paradigms. The effect has been observed during the learning of word lists [10, 12, 22], images [9], paired associates [23], and spatial information [24], and it emerges whether memory is tested via free recall [12, 22, 25] or recognition [9, 26].

Alpha and gamma-band SMEs have been robust across recording methods, including scalp EEG [10, 12, 22], MEG [27], and intracranial EEG [12, 28, 29]. As discussed in Box 1, theta activity has had mixed associations with encoding, usually predicting successful memory in scalp EEG [10, 12, 22], and sometimes emerging only after the application of IRASA correction in intracranial EEG [15]. Across these methods, $T^+A^-G^+$ is consistently observed as a spatially distributed effect, though its component frequencies show partially distinct topographies

Some of the most theoretically informative evidence regarding what $T^+A^-G^+$ actually captures was presented by Long and Kahana [30], who examined whether spectral activity could predict not only whether an item would be recalled, but whether it would be *temporally clustered*, or recalled contiguously with its list neighbors. If $T^+A^-G^+$ merely captured attentional engagement with the task, then it might predict whether an item will be recalled later, but not *how* that item is recalled. Using scalp EEG recordings, the authors reported that increased low-theta and gamma activity distinguished between subsequently clustered and nonclustered items, while alpha did not. This pattern suggests that theta and gamma track the binding of items to their encoding context, beyond what attention and arousal alone would predict.

Retrieval

If $T^{+}A^{-}G^{+}$ only reflects increased attention to incoming external stimuli during encoding, then it should not be observed during retrieval, where no new items are being presented. As we review below, the evidence for $T^{+}A^{-}G^{+}$ during retrieval is robust, and in many cases more consistent than that reported in the encoding literature.

Katerman et al. [25] demonstrated $T^{+}A^{-}G^{+}$ at retrieval by contrasting the neural patterns immediately preceding spontaneous free recall with activity from matched **deliberation periods**, in which participants were presumably engaged in memory search but not actively recalling any items. This analysis revealed a diffuse, bilateral $T^{+}A^{-}G^{+}$ pattern predicting successful retrieval. Dougherty et al. [24] replicated this finding within a naturalistic spatial learning task, with $T^{+}A^{-}G^{+}$ robustly expressed diffusely across scalp regions. However, a significant limitation of this contrast is that we cannot know what mental processes occur during the deliberation intervals. Participants may be actively searching memory, passively mind-wandering, or doing something else entirely. As a result, this contrast does not cleanly isolate memory-specific processes from differences in cognitive effort or task engagement.

Katerman and colleagues sought to address this limitation by contrasting the delayed recall of an item encoded during a previous testing session with the earlier immediate recall of that same item moments after it was shown onscreen. This contrast kept motor demands constant across conditions, thereby isolating the memory-specific demands of long-term retrieval from task-general demands of premotor planning. Again, a robust $T^{+}A^{-}G^{+}$ effect predicted delayed free recall, though in this case the theta effects were expressed in the anterior electrode sites, while gamma and alpha effects emerged most clearly over posterior scalp regions.

A more direct test of whether $T^{+}A^{-}G^{+}$ reflects memory-specific processes as opposed to task-general cognitive effort comes from contrasts of correct recalls vs. intrusion errors in free recall. Both response types involve effortful, generative retrieval attempts, but the quality of the underlying memory signal should differ between them. The first studies to examine this question used intracranial recordings, finding that elevated hippocampal gamma activity distinguished between correct and false recalls [13, 31]. Herz et al. [21] extended this finding, reporting the full $\mathrm{T}^{+}\mathrm{A}^{-}\mathrm{G}^{+}$ profile in the hippocampus during correct recalls relative to intrusions. From scalp EEG recordings, Li et al. [32] replicated the gamma and alpha components of this pattern. These studies argue that $\mathrm{T}^{+}\mathrm{A}^{-}\mathrm{G}^{+}$ captures something more than just cognitive effort and engagement, because it distinguishes accurate from inaccurate memories even when both involve active response generation. Other approaches have shown that pre-recall spectral activity also reinstates contextual information associated with the to-be-recalled item [33–35], indicating that this activity carries memory-specific information about encoded events beyond what response generation can explain.

The above findings demonstrate an overlap between encoding and retrieval processes. Kragel et al. [36] formalized this correspondence by showing that logistic classifiers trained on retrieval could successfully predict encoding and vice versa. However, $\mathrm{T}^{+}\mathrm{A}^{-}\mathrm{G}^{+}$ effects tend to more reliably predict retrieval than encoding [24, 36]. The authors theorized that items that are successfully encoded may nonetheless fail to be retrieved during testing. Even the clearest, most directly causal signal of successful encoding might not predict how subsequent interference might disrupt the memory trace later on. By contrast, the neural signal at retrieval more directly maps onto the behavioral outcome, because it is assessed only a few hundred milliseconds before a response.

A unified mechanism, or dissociable processes?

If $\mathrm{T}^{+}\mathrm{A}^{-}\mathrm{G}^{+}$ emerges through a single mechanism, then its components should behave consistently across space, time, and task demands. In the following section, we consider evidence both for and against this theory.

Spatial specificity

Although $T^{+}A^{-}G^{+}$ is commonly spatially diffuse in scalp EEG, some reported topographic differences hint at dissociability. As noted earlier, when Katerman et al. [25] contrasted delayed vs. immediate free recall, they found that the theta component was primarily expressed over frontal scalp regions, while alpha and gamma effects were concentrated at posterior scalp sites. This anterior-posterior distinction is not unique to retrieval. Both Friese et al. [9] and Osipova et al. [26] found a similar pattern during picture learning, reporting that successful encoding was predicted by increased frontal theta power coupled with decreased posterior alpha and increased posterior gamma.

This regional differentiation among the core components of $T^{+}A^{-}G^{+}$ is more pronounced in intracranial recordings. Theta SMEs are commonly seen within hippocampal and frontal brain areas, while gamma positivity is more broadly distributed across the temporal, occipital, and frontal cortices [6, 8, 12, 37]. Greenberg et al. [38] extended these observations to a paired-associate task, reporting a posterior-to-anterior progression of gamma increases across the encoding period. Meanwhile, alpha suppression demonstrates little differentiation among brain regions. This greater spatial specificity among gamma and theta effects compared to alpha suppression hints at their greater sensitivity to task demands, as we will discuss below. Herweg et al. [14] discussed the scalp-intracranial discrepancy, remarking that scalp electrodes aggregate their signal over a far larger cortical area than intracranial sites, capturing both signal amplitude and its synchronization across broad regions. This methodological difference means that scalp-based $T^{+}A^{-}G^{+}$ can appear spatially diffuse even when underlying generators are regionally specific.

Temporal dynamics

A single underlying mechanism of $T^{+}A^{-}G^{+}$ should cause its components to emerge uniformly across time, increasing during periods of high memory performance. We should therefore see the $T^{+}A^{-}G^{+}$ components appear together both within study trials and across

serial positions during encoding.

Consistent with this prediction, some studies have reported that $T^+A^-G^+$ emerges approximately uniformly within encoding trials, including during prestimulus periods [39, 40]. However, other studies have reported within-trial temporal dissociations among the components. Specifically, while gamma effects were consistent across trial periods, alpha SMEs tended to emerge roughly 500 ms after trial onset [22, 26, 27]. A possible interpretation is that gamma reflects a state of sustained attention and readiness to encode, while alpha suppression reflects rapid orientation to the study item after it appeared. However, these mixed findings within the literature remain unresolved, and could reflect differences in study paradigms or analysis methods.

Across serial positions, clearer dissociations emerge between gamma and alpha activity. Predictions regarding how $T^+A^-G^+$ should behave across serial positions are complicated by the ongoing debate about whether primacy effects capture increased attention due to a context boundary [41, 42], or if they merely reflect increased rehearsal of early list items across the encoding period, irrespective of superior online encoding [43, 44]. These accounts make different predictions about whether $T^+A^-G^+$ should be strongest at early serial positions.

Regardless of these competing theories, the predictive value of $T^+A^-G^+$ components varies across serial positions even when the overall $T^+A^-G^+$ signature does not. The full pattern of elevated theta, suppressed alpha, and elevated gamma is most strongly expressed early in lists and weakens across subsequent item presentations. However, the SMEs derived from these components do not uniformly mirror this trajectory. The gamma SME is strongest at early serial positions and weakens across the list, while the negative alpha SME strengthens across the encoding period [29, 32, 45]. The theta component follows a less clear trajectory given its mixed associations with successful memory formation, but scalp EEG evidence suggests that the positive low-theta SME mirrors that of gamma [45]. If $T^+A^-G^+$ captured a single mechanism, the components' predictive value should rise and fall together across serial positions. Instead, the alpha SME moves in opposite directions from that of theta and gamma. One explanation could be that theta and gamma reflect focused encoding early in a list, when attentional demands are minimal, while alpha suppression reflects the recruitment of additional processing resources as competing demands build up across the list. This pattern fits with the spatial differences described above and, as we discuss next, the components' differing responses to task demands.

Variability across task demands

In addition to consistencies across time and topography, a single mechanism of $T^+A^-G^+$ would predict its components to uniformly vary across task demands. Several dual-task studies have shown the effects to vary with cognitive demands, however the components were not all equally affected.

Broitman and Swallow [22] examined scalp EEG during word list encoding under single-task and divided-attention conditions, finding that a concurrent target detection task markedly weakened gamma SMEs while alpha and theta effects persisted. Broitman et al. [10] replicated and extended this finding using a concurrent semantic judgment task, observing significant weakening of both theta and gamma under divided attention while the alpha SME again remained robust. Long and Kahana [30] further showed that the semantic task weakened subsequent clustering effects in the theta and gamma frequencies, but not alpha. The consistent robustness of alpha SMEs across these manipulations contrasts with the selective weakening of theta and gamma effects, indicating that the components vary independently with cognitive demands.

Individual differences

Few studies have directly investigated differences among individuals in spectral biomarkers of memory. However, the available data speak to the view that $T^+A^-G^+$ reflects the joint operation of dissociable processes.

Broitman et al. [10] compared scalp EEG SMEs in young adults (age 18-30) with those of older individuals (age 61-85). The authors reported an overall weakening of the $T^+A^-G^+$ effect among older adults, proposing that this may reflect inhibitory deficits that reduce the ability to retain focused states of sustained attention [46–48]. According to this theory, older adults are less able to induce the cognitive states captured by $T^+A^-G^+$ during encoding, and their memory suffers as a result. An alternative explanation is that, instead of capturing encoding deficits, a weakened $T^+A^-G^+$ SME among older adults reflects increased susceptibility to interference between study and test. If normal age-related memory deficits stem more from failures of retrieval than encoding, as suggested by the literature [49–51], then $T^+A^-G^+$ activity may remain relatively intact at encoding while still being a poor predictor of future recall.

Both interpretations of the above findings are consistent with the view that a stronger $T^+A^-G^+$ SME reflects better memory, and suggests individuals with more intact neural machinery present a greater $T^+A^-G^+$ response and remember more. This intuition is sharply contrasted by findings that, among young adults, the effect actually *weakens* in people with better memory performance [32]. Sheehan et al. [52] reported a similar pattern in intracranial recordings from a paired-associate task, with high-performing individuals exhibiting less broadband power and flatter power spectral density slopes than low performers. This convergence across scalp and intracranial recordings suggests that weakened spectral biomarkers reflects a consistent feature of good learners.

Resolving these contradictory findings requires distinguishing between different reasons for why the $T^+A^-G^+$ SME can be weak. Among older adults, weakened $T^+A^-G^+$ could reflect some combination of degraded neural machinery and retrieval impairments. The memory system might be less able to induce optimal encoding states when they are needed, or these states are less predictive of behavioral outcomes. Either way, the weakened SME among older adults points to some form of memory disruption. Among high-performing young adults, weakened $T^+A^-G^+$ may reflect reduced variability in encoding states across trials. Because the SME contrasts activity between remembered and forgotten items, it depends not on the overall level of $T^+A^-G^+$ but on the difference between these conditions. High-performing individuals' neural states may vary less across trials, making recall outcomes less predictable from trial-level activity. A weak $T^+A^-G^+$ effect here reflects a reduction in the variability that produces SMEs rather than weakness in the underlying encoding processes.

An informative test for both hypotheses would be to compare $T^+A^-G^+$ effects between individuals at retrieval. If older adults or high-performing young adults exhibit preserved $T^+A^-G^+$ effects during successful recall despite weakened encoding SMEs, this would suggest that the neural processes underlying $T^+A^-G^+$ remain functional and that the weakened encoding contrast reflects either decoupling from behavioral outcomes (in older adults) or reduced trial-level variability (in high performers). To our knowledge, neither comparison has been reported, and they represent important empirical gaps.

Unlike studies comparing $T^+A^-G^+$ across time, task demands, and spatial regions, the individual differences literature does not cleanly support the dissociability hypothesis. When $T^+A^-G^+$ weakens among better learners or older adults, all three components weaken together, which is more consistent with a unified mechanism than dissociable processes. One possibility is that the components behave independently across different experimental conditions, but co-vary when measured as stable traits across individuals. An important direction for future research will be to address the question of why $T^+A^-G^+$ components appear dissociable across experimental task manipulations but not necessarily across individuals.

Is $T^+A^-G^+$ memory-specific?

The previously reviewed evidence establishing $T^+A^-G^+$ as a biomarker of memory across a wide range of mnemonic tasks does not settle the question of whether this activity is specific to episodic memory. If the full $T^+A^-G^+$ pattern reflects only generic cognitive effort or cortical arousal, it should track these variables across many tasks and contexts, including those without any memory demand. If it instead reflects memory-specific processing, it should carry information about the underlying memory signal that pure effort or arousal accounts cannot explain, and it should arise only during memory-relevant tasks.

As discussed earlier, there is evidence to suggest that the full $T^{+}A^{-}G^{+}$ pattern captures something more than just cognitive effort or task engagement. $T^{+}A^{-}G^{+}$ activity reliably distinguishes between correct recalls and intrusion errors even though both involve effortful and generative attempts at retrieval [13, 21, 31, 32]. The finding that low-theta and gamma distinguish subsequently clustered from nonclustered items [30, 32] is also difficult to explain under a pure effort account, which has no reason to predict the temporal organization of recall. Together, these findings suggest $T^{+}A^{-}G^{+}$ reflects features of memory that go beyond whether retrieval succeeds.

Whether $T^{+}A^{-}G^{+}$ generalizes beyond episodic memory remains less clear. Several studies have observed $T^{+}A^{-}G^{+}$ -like activity during working memory maintenance. van Vugt et al. [53] reported the full $T^{+}A^{-}G^{+}$ pattern in the hippocampus and medial temporal lobe scaling with load during a Sternberg working memory task. Scalp EEG studies applying aperiodic decomposition have reported similar findings, with alpha decreases and theta-gamma coupling effects emerging during working memory retention [37, 54, 55]. However, the cognitive processes involved in working memory and episodic encoding overlap substantially, including item-context binding and short-term retention. These findings therefore do not show that $T^{+}A^{-}G^{+}$ arises in the absence of episodic processing, but they suggest that it extends to memory-relevant processes more broadly. Reports of $T^{+}A^{-}G^{+}$ -like activity following visual target detection [22, 56] face a similar interpretive challenge, since target detection itself has been proposed to enhance episodic encoding through noradrenergic mechanisms [57]. As a result, it is difficult to determine whether $T^{+}A^{-}G^{+}$ appears during non-mnemonic processing.

Some non-mnemonic tasks produce a spectral pattern that resembles parts of

$T^+A^-G^+$. Motor movements produce cortical alpha desynchronization coupled with broadband high-frequency increases [58], which subsequent decomposition methods identified as a broadband $1/f$ spectral tilt rather than coordinated narrowband oscillations [59]. The simple act of opening the eyes suppresses alpha [1, 60], and the broader spectral tilt distinguishes wakefulness from sleep [61]. These contrasts implicate alpha suppression and broadband gamma activity, but narrowband low-theta has not been systematically linked to motor execution, eye opening, or arousal-state changes. To our knowledge, no studies have reported the full joint $T^+A^-G^+$ pattern in contrasts that experimentally isolate non-mnemonic cognitive demands, though the available literature has rarely tested this directly. Whether $T^+A^-G^+$ emerges during effortful tasks that neither require nor enhance episodic memory therefore remains an open empirical question.

A component theory of $T^+A^-G^+$

If $T^+A^-G^+$ captures something beyond generic cognitive effort, then this raises the question of how each component contributes to episodic memory. Prior literature reviews have discussed the functional roles of theta, alpha, and gamma oscillations in human memory [14, 62, 63]. Here, we build on that work by proposing that $T^+A^-G^+$ reflects the joint activation of multiple, partly dissociable processes which vary in their degree of memory specificity. This theory has precedent from Fellner et al. [27], who examined spatial and temporal differences in SMEs and found that dissociable spectral "fingerprints" underlie frequency-specific memory effects. The current review expands on this position by including evidence from individual differences, dual-task manipulations, and serial position dynamics to better characterize the nature of these processes.

Oscillatory theta

We propose that theta oscillations play the most direct role in supporting episodic memory among the components of $T^+A^-G^+$. Theta oscillations are often localized to hippocampo-cortical networks during memory tasks [64, 65], and synchronized theta creates favorable conditions for long-term potentiation and synaptic plasticity [66–68]. If our proposal is correct, theta SMEs should depend on the availability of these binding circuits beyond what cognitive load alone would predict.

Consistent with this view, the theta SME is sensitive to manipulations that tax hippocampal resources. Theta SMEs weakened when participants performed a concurrent semantic judgment task, which is known to recruit fronto-temporal networks [69], but persisted under a target detection task that merely diverts attentional resources from encoding [10, 22, 30]. While this comparison spans separate studies and warrants further direct testing, it supports the possibility that theta SMEs depend on the availability of specific neural circuits involved in item-context binding rather than tracking cognitive load alone. Converging fMRI evidence has shown that hippocampal BOLD activity predicts successful encoding under single-task conditions, but not when encoding is accompanied by a secondary semantic processing task [70].

Box 2. Theta-Gamma Coupling Supports Item-Context Binding

How does the brain organize and bind multiple items into an episodic representation? Lisman [71] proposed that gamma cycles nested within slower theta waves provide a neural code for simultaneously representing multiple items in mind. Sparse assemblies of neurons representing individual items fire synchronously at a gamma rhythm, while the phase of the theta cycle determines the sequence in which these items are activated. Gamma and theta activity thereby function as coupled components of a single memory-binding mechanism [72–74].

Several human intracranial EEG studies have presented evidence of a theta-gamma coupling mechanism. Burke et al. [19] demonstrated that both synchronous and asynchronous theta and gamma predicted successful episodic memory formation with gamma showing more asynchrony and theta showing more synchrony. Later studies found that slow-wave hippocampal theta modulates gamma activity via phase-amplitude coupling, and this effect strengthens during successful memory formation [37, 75]. More recent work has shown that hippocampal gamma couples to opposing theta phases during learning and recall, suggesting that the theta cycle can organize item representations and shift the brain between states that support encoding vs. retrieval [76]. However, theta-gamma coupling does not by itself establish that the high-frequency component is narrowband oscillatory, since theta phase can also modulate the amplitude of broadband activity [19, 77].

Gamma-band activity

A key question regarding gamma is whether this activity reflects oscillatory or aperiodic processes. Most intracranial gamma-band SMEs have been shown to capture broadband high-frequency activity [19, 78]. However, studies using oscillation-detection methods have identified a small subset of hippocampal electrodes with genuinely narrowband gamma SMEs [8, 77], and oscillatory gamma has been shown to distinguish correct from false recalls [21]. To the extent that true oscillatory gamma contributes to memory processes, it likely functions as part of a theta-gamma coupling mechanism that supports item-context binding (see Box 2).

Broadband gamma probably captures a more task-general cognitive mechanism than oscillatory low-theta. This activity has been proposed to reflect pooled neuronal spiking and local computational activity [79]. As noted earlier, it forms part of the spectral tilt pattern that predicts cortical processing across motor, sensory, and arousal contexts [58, 78, 80]. Consistent with this, the gamma-band SME is sensitive to competing cognitive demands, weakening under both target detection and semantic dual-task conditions [10, 22] and declining across serial positions as encoding demands increase [45]. Gamma is nonetheless a robust component of $\mathrm{T}^{+}\mathrm{A}^{-}\mathrm{G}^{+}$, because successful episodic encoding and retrieval typically require the effortful recruitment of neural computational resources. Its association with successful encoding weakens under divided attention precisely because those resources are diverted elsewhere.

Related to gamma-band activity is the hippocampal **sharp-wave ripple**. Although ripples occur within the gamma frequency range, they are transient oscillatory events rather than sustained broadband activity, and their functional significance differs from that of broadband gamma (see [81] for a review). Recent work has shown that encoding ripples do not distinguish subsequently recalled from forgotten items in the manner of an SME. Instead, hippocampal ripples during encoding predict whether items will be recalled in temporal and semantic clusters [82, 83]. Beyond encoding, hippocampal ripples have been more strongly tied to memory retrieval, with sharp-wave ripples preceding successful episodic retrieval [84, 85]. These findings link ripples more closely to the item-context binding processes captured by theta and narrowband gamma than to the general computational demands indexed by broadband activity. One limitation of scalp EEG is that it cannot reliably distinguish between broadband, oscillatory, or ripple-like gamma activity, as doing so typically requires intracranial recordings paired with advanced analytical techniques like IRASA or ripple-detection pipelines. Many of the gamma-band effects reviewed in this article may therefore capture a mixture of all three types of activity, and future work will be needed to disentangle their respective contributions to $\mathrm{T}^{+}\mathrm{A}^{-}\mathrm{G}^{+}$.

Alpha

Alpha suppression is the most robust and, we argue, the least memory-specific component of $\mathrm{T}^{+}\mathrm{A}^{-}\mathrm{G}^{+}$. As discussed previously, alpha suppression captures general cortical engagement across many non-mnemonic contexts [58, 61]. Within memory tasks, the alpha SME persists under divided attention conditions that eliminate theta and gamma effects [10, 22], and it strengthens across serial positions as the other components weaken [29, 45]. These properties suggest that the alpha SME operates even when encoding-specific resources are depleted.

One interpretation of alpha suppression is that it reflects increased perceptual processing. Supporting this account are findings that event-related alpha desynchronization is most pronounced over visual processing areas [86] and that alpha power increases with working memory load, possibly reflecting attenuated processing of incoming stimuli to prioritize internal representations [87, 88]. However, a purely perceptual account is complicated by the finding that alpha suppression immediately precedes spontaneous recall [24, 25, 89]. During a recall period, no new stimuli are being presented, and increased engagement with the external environment has no bearing on task performance. If alpha suppression only captures perceptual gating, then it should not emerge in this context.

We propose instead that alpha suppression marks the phasic mobilization of a neural effector system. This system releases task-relevant cortical regions from baseline inhibition when discrepancies arise between an individual's internal state and the demands of the task environment. During recall, for example, a participant may be in a passive resting state while the task requires active memory search. Alpha suppression may capture the brain's detection of this mismatch and its subsequent recruitment of the processes needed to resolve it. This framework predicts that alpha suppression should weaken in contexts where the cortical state already supports task demands. Consistent with this prediction, alpha activity remains elevated during well-practiced task performance [90, 91], even when engagement, perception, and working memory load remain high. Our framework extends existing inhibitory-gating accounts [86, 92] by specifying not only what alpha modulates (cortical inhibition) but also when and why it does so (phasic, in response to state-task mismatches).

A potential complication for this task-general framing is the finding that alpha suppression distinguishes correct recalls from intrusion errors [21, 32]. However, alpha's role need not be memory-specific to be memory-relevant. Hippocampo-cortical binding mechanisms require an actively engaged cortical system, and alpha suppression may help establish that engagement without directly performing the binding itself. Alpha suppression may instead mark the transition from a resting state into active cortical engagement.

The overall specificity of T^{+}A^{-}G^{+} to episodic memory is therefore graded rather than binary, depending on which component one examines. Oscillatory theta and theta-coupled gamma are the strongest candidates for a memory-specific component, given their sensitivity to hippocampal activity and item-context binding. Broadband gamma, meanwhile, reflects task-general local neural recruitment. It is a robust component of T^{+}A^{-}G^{+} because successful episodic encoding and retrieval often require effortful and demanding cognitive operations. Finally, alpha suppression may be the least memory-specific component, capturing the automatic mobilization of neural resources. Although no single component is entirely memory-specific on its own, their joint occurrence may be more specific to mnemonic processing than any one alone. This explains why T^{+}A^{-}G^{+} reliably emerges during episodic memory tasks, but does not speak to its causal role. We discuss this question in Box 3.

Box 3. Does T^{+}A^{-}G^{+} reflect a *causal* signal of memory?

If T^{+}A^{-}G^{+} captures a causal signal, then interventions that increase it should improve memory. If it is only correlational, then therapies targeting T^{+}A^{-}G^{+} would be misguided, irrespective of its predictive value.

Evidence from the brain stimulation literature preliminarily supports a causal role. Ezzyat et al. [28] showed that direct brain stimulation had state-dependent effects on memory. Stimulation delivered during poor encoding states increased gamma activity, suppressed alpha, and improved subsequent recall relative to sham treatment, whereas stimulating during good encoding states disrupted memory. **Closed-loop** extensions of this work, in which neural classifiers trigger stimulation only when poor memory is predicted, rescued periods of poor encoding and improved recall performance [93, 94]. These findings indicate that the neural states captured by spectral SMEs can be externally modulated to improve memory.

More recently, Rudoler et al. [95] developed a closed-loop system that used scalp EEG classifiers to control the timing of stimulus presentation, presenting study items during predicted good ("optimize") or poor ("impair") encoding states. Although this manipulation did not improve memory at the group level, classifier performance varied considerably across participants due to insufficient training data. Among those whose classifiers performed well (AUC $>$ .60), recall was significantly higher in the optimize condition vs. impair. It is therefore plausible that manipulating stimulus timing based on spectral SMEs can modulate memory.

Together, these findings suggest SMEs reflect more than passive correlates of encoding. However, because these studies relied on broadband multivariate spectral features rather than band-specific $T^{+}A^{-}G^{+}$ components, it remains unclear whether the memory benefits arose from modulating theta, alpha, gamma, or some combination thereof. Future closed-loop approaches that selectively target individual $T^{+}A^{-}G^{+}$ components would provide a more precise test of our component theory. If theta-gamma and alpha reflect dissociable processes, then targeting each through rhythmic stimulation should produce dissociable effects on memory [96].

Even if the causal status of $T^{+}A^{-}G^{+}$ remains uncertain, spectral SMEs could still have diagnostic utility for classifying brain states. Fukuda and Woodman [97] measured scalp EEG frontal positivity and occipital alpha to flag study items that were poorly encoded, then had participants restudy those items. Items flagged as poorly encoded showed greater memory benefit from restudy than items flagged as well-encoded, indicating that the EEG biomarkers identified meaningful variation in encoding states. This kind of application does not require resolving the causality question, only that the signals can predict which items or states warrant intervention.

Concluding remarks

Our review of the literature on $T^{+}A^{-}G^{+}$ has sought to address two key questions: 1) Whether it represents the activation of a single neural mechanism, or multiple dissociable neural processes, and 2) whether it captures memory-specific processing as opposed to a task-general index of cognitive engagement. The available evidence speaks to both. The components of $T^{+}A^{-}G^{+}$ dissociate across serial positions, spatial topography, and task demands, arguing against a single unified mechanism. The pattern also predicts item-context binding, distinguishes correct recalls from intrusions, and shows frequency-specific dissociations that are difficult to explain under a pure effort account. We therefore propose a component theory in which $T^{+}A^{-}G^{+}$ reflects the joint activation of multiple, partly dissociable processes that vary in their degree of memory specificity. Low-theta and theta-coupled gamma appear most closely tied to item-context binding through hippocampo-cortical coordination, broadband gamma likely reflects the general recruitment of computational resources, and alpha suppression may capture a task-general effector process.

Outstanding Questions

- $T^{+}A^{-}G^{+}$ components appear dissociable across time and experimental manipulations, but tend to co-vary across individuals. Why is this, and are there certain component frequencies that might selectively vary across individual differences?
- Do weakened SMEs in older adults represent changes in how these individuals learn, or a reduced correspondence between encoding-related activity and later retrieval due to increased interference?
- Does the $T^{+}A^{-}G^{+}$ pattern generalize to other cognitively challenging, non-mnemonic tasks? Would the pattern predict mathematical problem solving or performance on a Stroop task?

- Does $T^{+}A^{-}G^{+}$ reflect neural processes that causally support memory, or is it merely a passive correlate of mnemonic success?

Author Note

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Glossary

Alpha. Spectral activity in the 8–12 Hz frequency range. Alpha desynchronization (a decrease in power) has been associated with active cortical engagement, attentional orienting, and the release of task-relevant neural populations from inhibition.

Aperiodic activity. Non-oscillatory background component of the neural power spectrum, characterized by a $1/f$ power-law distribution. Also referred to as broadband or fractal activity. Reflects pooled neuronal spiking and is dissociable from narrowband oscillations using decomposition methods such as IRASA (See below).

Broadband gamma. Non-oscillatory high-frequency activity (typically >30 Hz) that reflects pooled local neuronal spiking and general cortical arousal. Distinct from narrowband oscillatory gamma.

Closed-loop stimulation. Experimental paradigm in which neural activity is monitored in real time and interventions (such as electrical stimulation or stimulus presentation) are triggered based on decoded brain states.

Deliberation period. An interval during free recall in which the participant is engaged in memory search but does not produce a response. Used as a control condition against which successful retrieval events can be contrasted.

Gamma. Spectral activity above 30 Hz, sometimes divided into low gamma (30–50 Hz) and high gamma (>50 Hz). May reflect either narrowband oscillatory activity or broadband aperiodic activity, depending on the signal.

IRASA. Irregular resampling auto-spectral analysis. A method for separating the periodic (oscillatory) and aperiodic (broadband) components of the neural power spectrum by exploiting the fractal properties of the aperiodic background.

Narrowband gamma. Oscillatory gamma-band activity concentrated at a specific frequency, distinct from broadband gamma. Often coupled to theta phase and implicated in hippocampal item-context binding processes.

Oscillations. Rhythmic neural activity concentrated at a specific frequency, distinguishable from aperiodic (broadband) activity as a spectral peak above the $1/f$ background. Often used interchangeably with "narrowband activity," in contrast to broadband or aperiodic signals.

Serial position. The ordinal position of a given item within an encoding list. Recall performance typically depends on serial position, with enhanced memory for early (primacy) and late (recency) list items.

Sharp-wave ripple. Transient, high-frequency (80–150 Hz) oscillatory event originating in the hippocampus. Associated with memory consolidation, replay of prior experience, and the organization of recall.

SME. Subsequent memory effect. A difference in neural activity during encoding between items that are subsequently remembered and those that are subsequently forgotten. The core paradigm used to identify neural correlates of successful memory formation.

Spectral $\mathbf{T^{+}A^{-}G^{+}}$. A pattern of spectral activity that predicts successful episodic memory encoding and retrieval, characterized by increased low-theta power (3–5 Hz), decreased alpha power (8–12 Hz), and increased gamma power (> 30 Hz).

Theta. Spectral activity in the 3–8 Hz range. Often subdivided into slow theta (3–5 Hz), which has been linked to hippocampo-cortical memory processes, and fast theta (7–8 Hz), which behaves more like alpha-band activity.