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7   EEG biomarkers of free recall

9   Katerman, B. S., Li, Y., Pazdera, J. K., Keane, C., and Kahana, M. J.

10   University of Pennsylvania

23   Author Note

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26   J. Kahana (kahana@psych.upenn.edu).

28   Abstract

Brain activity in the moments leading up to spontaneous verbal recall provide a

window into the cognitive processes underlying memory retrieval. But these

same recordings also subsume neural signals unrelated to mnemonic retrieval,

such as response-related motor activity. Here we examined spectral EEG

biomarkers of memory retrieval under an extreme manipulation of mnemonic

demands: subjects either recalled items after a few seconds or after several days.

This manipulation helped to isolate EEG components specifically related to long-

term memory retrieval. In the moments immediately preceding recall we

observed increased theta (4-8 Hz) power (+T), decreased alpha (8-20

Hz) power (-A), and increased gamma (40-128 Hz) power (+G), with this

spectral pattern (+T-A+G) distinguishing the long-delay and immediate recall

conditions. As subjects vocalized the same set of studied words in both

conditions, we interpret the spectral +T-A+G as a biomarker of episodic memory

retrieval.

Keywords: **theta, gamma, alpha, retrieval, reinstatement**

46   EEG biomarkers of free recall

48   **Introduction**

Our ability to recall past experiences is the hallmark of episodic memory. In laboratory studies,

lists of discrete nameable items, such as words, serve as sets of mini-experiences, and the act of recall is

the motor output (vocalization or typing) of the remembered items. The magic of memory retrieval

happens during the moments leading up to the motor output, but this period also includes other non-

mnemonic signals, such as the planning of a motor response and the activation of semantic and

perceptual representations associated with the remembered item.

Prior research using intracranial EEG recordings has uncovered a network of brain regions in

which increased high frequency activity and concomitant decreases in lower frequency activity mark the

moments leading up to spontaneous verbal recall as compared with matched periods of silence during

the recall period (Burke, Sharan, et al., 2014; Greenberg, Burke, Haque, Kahana, & Zaghloul, 2015;

Solomon et al., 2017). In some cortical sub-regions and for some retrieval contrasts, low-frequency (3-8

Hz) theta activity increases during the putative retrieval period (see Herweg et al., 2016, for a review).

Researchers would ideally like to use these recall biomarkers to probe the dynamics of memory retrieval

in the absence of motor output.   Such signals could, for example, be used to study the hypothesized

role of covert retrieval in memory consolidation and other learning processes.   However, the

interpretation of these recall biomarkers is problematized by the concomitant presence of non-

mnemonic neural processes that accompany recall even under minimal memory demands.

Comparisons of correct and incorrect recalls (intrusions) offers a potential solution (Long et al.,

2017) These studies have shown, for example, that hippocampal high-frequency activity increases

moreso prior to correct recalls than prior to intrusion errors.   As incorrect recalls presumably involve

identical, or at least very similar, motor planning activity, differences between these conditions more

likely reflect mnemonic retrieval.   However, intrusions may show similar signals to those of successful

recall as the subject is actively engaged in recall of a word they believe to have been previously

presented. As such, these contrasts may mask important neural correlates of memory retrieval that

appear similarly for both true and false memories.

The present study sought to elucidate the biomarkers of episodic memory retrieval by

examining recall of words under an extreme manipulation of retrieval demands: In an immediate recall

condition, subjects recalled a single just-presented word after a brief delay.   In a long-delayed recall

test, subjects attempted to recall items learned across multiple days prior to the test day (i.e., a

minimum of 16 hours prior to the recall period). Over the course of ten experimental sessions

administered on different days, subjects contributed data in each of these conditions.

81   **Method**

Subjects

Fifty-seven young adults (ages 18-35, 24 reported male, 29 reported female, 53 reported right-

hand dominant), recruited among the students and staff at the University of Pennsylvania and

neighboring institutions, each contributed 10 sessions of immediate word recall data and five sessions of

delayed recall data. All subjects provided informed consent to participate in our study, which was

approved by the Institutional-Review Board at the University of Pennsylvania. Subjects were excluded

(n=17) if they did not complete at least 7 sessions or if they had an average rate of recall lower than 70%

during the immediate recall task. The data reported here came from Experiment 5 of the Penn

Electrophysiology of Encoding and Retrieval Study (PEERS). This is the first paper to report data from

PEERS-Experiment 5.

Data Availability

All PEERS data, including the full dataset reported and analyzed in the present manuscript, may

be freely downloaded from our public repository http://memory.psych.upenn.edu/data. Analysis code

for this manuscript is also available at the same URL.

Experimental Task and Behavioral Analyses

Each of the first five sessions (henceforth, *Phase I*) consisted of one block of 10 practice trials,

followed by 24 blocks of 24 trials each. Each block began with a 10-second countdown. After the

countdown was complete, the first trial of the block began. On each trial, a black screen was shown for

a jittered 1000--1600 ms (uniformly distributed), after which a single word appeared onscreen in white

text for 1200--1800 ms (uniformly distributed). Following presentation, the screen went blank again and

subjects were instructed to pause briefly, and then vocalize the word they had just seen. If they began

speaking within 1.0 seconds of word offset, the message "Too fast." appeared on the screen in red text.

By avoiding these messages subjects could increase the size of their bonus payment.   After the subject

finished speaking, a tone sounded, marking the end of the current trial. Speech was detected using a

volume amplitude threshold. In addition to the 10-second countdown between blocks, two 2-minute

mid-session breaks were administered after block eight and block 16.

Phase II of the experiment began on the day of the sixth session and continued to the final

session of the experiment. In Phase II the practice block and 24 experimental blocks were preceded by a

10-minute initial externalized free recall period. Subjects were instructed to recall as many words as

possible from the previous sessions in any order, while also vocalizing any additional words that come to

mind in their attempt to recall these items (e.g., Kahana, Dolan, Sauder, & Wingfield, 2005; Lohnas,

Polyn, & Kahana, 2015; Zaromb et al., 2006). Our lists comprised the same 576-word pool as used in the

PEERS4 study (Aka, Phan, & Kahana, 2020; Kahana, Aggarwal, & Phan, 2018; Weidemann & Kahana,

2020). Subjects saw the same 576 words in each of their 10 sessions, but the ordering of these words

was randomized for each session. Although subjects saw the 576 words across multiple sessions, the

only information identifying these words as belonging to the target list was their occurrence within the

context of our experiment, thus making this a test of long-term episodic memory.

EEG Post-Processing and Spectral Decomposition

We recorded electroencephalographic (EEG) data using a 128-channel Biosemi system with a

2048 Hz sampling rate. We applied the following preprocessing steps to the data from each session.

First, we applied a 0.5 Hz highpass filter to eliminate baseline drift. We then partitioned the recording

into thirds by splitting at the end of each mid-session break.   For each partition of the data, we

identified bad channels as those with extremely high or low ($|z|>3$) log-variance, or which had an

extremely high ($z>3$) Hurst exponent relative to other channels. We identified bad channels separately

for each partition, as problematic electrodes were often corrected during mid-session breaks.[1] We then

dropped the bad channels from their respective partitions and applied a common average reference

scheme.   We next performed independent component analysis (ICA) on each of the three partitions to

decompose the data into 128-(n+1) components, where n is the number of bad channels that were

dropped, and used the localized component filtering method of DelPozo-Banos and Weidemann (2017)

to filter artifactual time points from the components. Data points were identified as artifacts if they

exceeded that component's interquartile range by three times the magnitude of that range. We then

reconstructed the original channels from the cleaned components, interpolated bad channels using

spherical splines, and applied a fourth-order Butterworth notch filter at 60 Hz to eliminate electrical line

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[1] Recordings during break periods were frequently noisy as a result of these adjustments and participant movement, and were therefore excluded when calculating variances and Hurst exponents, as well as when performing ICA and calculating artifact thresholds for localized component filtering.

noise.

We used a multitaper method (MNE-Python software package; Gramfort et al., 2013,2014) to

estimate spectral power at each electrode over 4--128 Hz and log transformed the resulting signal.

Electrodes were grouped into regions of interest (see Figure 2) and the corresponding powers averaged

for each frequency. We spaced frequencies every 2 Hz in the range of 4--26 Hz, and every 6 Hz within

26--128 Hz, resulting in 29 frequencies of interest. We avoided the Morlet wavelet method, as

convolving low frequency wavelets using buffer periods may allow speech artifacts to intrude in the

power estimates of intervals just prior to subjects' vocal responses. We used a 500 ms moving window

centered at multiple time-points relative to the start of recall events (i.e., vocalization of a recalled

item), with a 50 ms step size. To minimize potential artifacts from pre-motor activity, we extracted

spectral patterns in a 500 ms window ending 250 ms prior to the annotated time of speech onset unless

otherwise noted. We excluded from our analysis recall events that occurred within 1500 ms of the

onset of the prior recalled item. In addition to the interval preceding vocalization, we identified 1000

ms "deliberation" periods of silence during the delayed recall test that did not overlap with a preceding

vocalization (i.e., within 500 ms of vocalization onset) or a subsequent retrieval interval of interest.

Deliberation periods for both immediate and delayed recall contrasts were matched to recall events

using linear sum optimization, which minimizes the total time difference between recall events and

matched deliberation periods, and were constrained to events between the first and last delayed recalls

within a session.

During delayed recall, we defined successful memory events as the memory search intervals

immediately preceding recalls of list items (correct recalls). Unsuccessful memory search periods

preceded recall errors (i.e., intrusions from outside of the word pool: extra-list intrusions). To identify

spectral features specific to successful recall on the delayed recall test, we performed contrasts against

successful immediate recall and successful delayed recall across eight regions of interest (ROI). ROIs

were selected based on previous studies using similar EEG caps (Weidemann, Mollison, & Kahana,

2009). Only immediate recall events from the first ten minutes of the first five sessions were included in

these contrasts; this time period is matched to the delayed recall that occurs in later sessions and only

covers immediate recall events where the subject is unaware of future delayed recall tests. We also

performed a contrast between immediate recall events from the first five sessions and deliberation

periods from the long-delayed recall test using the same matching procedure. We aggregated desired

events from each session within subjects and performed a *t*-test to produce a variance-normalized

difference score for every frequency-by-ROI pair within subjects. We subsequently used two-tailed one

sample *t*-tests (with FDR correction) to assess group-level differences.

172   **Results**

Figure 1A illustrates the basic structure of the experiment. In each of 10 experimental sessions,

subjects performed a simple immediate-recall task. As each of 576 words appeared individually,

subjects read each word silently, and then, after a one second delay, recited the word aloud. At the

start of the 6th session (phase II), subjects were given a surprise long-delay recall task: We asked them

to recall as many of the 576 words as they could remember in any order as well as any words that come

to mind that may have not been presented in previous sessions. We then had subjects perform the

same immediate recall task as on previous sessions. Sessions 7-10 replicated the methods of Session 6

except that the initial recall test could no longer be deemed a surprise.

As expected, subjects recalled items with very high accuracy (above 96%) in the immediate

recall condition. Figure 1B illustrates accuracy of immediate recall across the 24 test blocks separately

for phases one and two. Accuracy fell slightly across blocks but recovered after each of the two-minute

breaks (see Figure 1A), possibly due to build-up and release from proactive interference (e.g., Lohnas et

al., 2015; Underwood, 1957). Figure 1C illustrates accuracy of long-delay free recall. On the first session

of phase II, subjects recalled an average of 29 words (5% of the total pool of 576 words). Their

performance on subsequent sessions increased dramatically, reaching an average recall rate of 103

items by the 10th session. This rate of increase (about 25 items per session) is much higher than the

implied rate of learning across sessions 1-5, but this likely reflects the difference between incidental and

intentional encoding.

Figure 1. **Experimental Paradigm and Behavioral Data. A.** During Sessions 1-5, subjects performed an

immediate recall task for each of 576 words, silently reading a word which they verbally recalled after

waiting approximately 1 second. On average, subjects responded 1.53 s after word onset. Each of

sessions 6-10 began with subjects attempting to freely recall the 576 words that they had seen on each

of the preceding sessions along with any other words that come to mind during a 10 minute retrieval

interval. Subjects then performed the same immediate recall task as on earlier sessions. **B.** Subjects

exhibited very high levels of immediate recall across all sessions, with performance dropping modestly

across blocks and recovering following breaks. **C.** Subjects exhibited modest levels of delayed recall on

the first (surprise) recall test given on Session 6, but performance rose sharply across subsequent

sessions, hitting an average of 103 correct recalls by the final session. **D.** Intrusions similarly rose across

sessions, but much less quickly than successful recalls. **E.** Inter-response times (IRTs) increased with

output position; on sessions where subjects recalled a larger proportion of items, IRTs were generally

faster throughout the retrieval period but rose sharply during the last few correct recalls.

Figure 1D illustrates the number of extra-list intrusions committed by subjects across the five

sessions of phase II. Here we see that subjects committed a much larger percentage of intrusions than

seen in standard within-session immediate and delayed recall tasks (Zaromb et al., 2006). However, the

overall fraction of intrusions decreased over sessions, dropping from 37% on Session 6 to 23% on

Session 10. Given the unusually-long delay in our free recall condition, and the very high rates of recall

achieved by the 10th session, we asked whether inter-response times (IRTs) across the recall period

exhibited the same pattern of growth as documented in more standard free-recall paradigms (Rohrer &

Wixted, 1994; Murdock & Okada, 1970). Figure 1E shows average IRTs based on the total number of

recalled words during delayed-recall sessions. This analysis demonstrates when subjects recall many

items, they exhibit much faster IRT overall. However, subjects still display a sharp increase in their IRTs

as they approach their final recalled item.

220   Our primary question concerned how neural activity, as measured through spectral analysis of

EEG recordings, signaled the process of spontaneous retrieval of previously experienced items. We first

addressed this question by comparing the 500 ms pre-vocalization period in the long-delay recall

condition with matched periods of silence separated by at least 0.5 sec from prior and subsequent

recalls (we refer to these as deliberation periods; see *Methods*). This comparison of retrieval and

deliberation periods revealed increased high-frequency activity and decreased alpha-band power across

most regions of interest (See Figure 2A; black outlined regions indicate statistically-significant frequency-

region pairs, FDR-corrected p<0.05), extending previous intracranial-recording studies that identified

similar retrieval biomarkers in both cued recall and free recall tasks (Burke, Ramayya, & Kahana, 2015;

Burke, Sharan, et al., 2014; Greenberg et al., 2015). Whereas those earlier studies examined recall that

took place within minutes of item encoding, the present study asked subjects to recall items that had

not been seen (experimentally) for at least 16 hours.

232   At anterior electrodes we observed increased theta-band activity during the pre-vocalization

memory-retrieval period. Although previous studies have frequently reported theta increases during

successful recognition memory (Addante, Watrous, Yonelinas, Ekstrom, & Ranganath, 2011; Guderian &

Düzel, 2005; Herweg et al., 2016; Osipova et al., 2006) most (standard) free recall studies find retrieval-

related *decreases* in theta and alpha-band power (Burke, Sharan, et al., 2014; Kragel, Koban, Barrett, &

Wager, 2018; Solomon et al., 2017; Solomon, Stein, et al., 2019). However, several free and cued recall

studies have found mixed results, with positive effects in specific brain regions, such as right anterior

temporal pole (Burke, Long, et al., 2014) and for specific contrasts, such as semantically-clustered vs.

non-clustered recall transitions (Solomon, Lega, Sperling, & Kahana, 2019). Our study demonstrates

retrieval-related increases in low theta power coupled with alpha-band decreases in a long-delay recall

task, conditions likely to place stronger demands on associative retrieval processes (Herweg, Solomon, &

Kahana, 2020).

Figure 2. **Statistical maps illustrating relative increases (red) and decreases (blue) in spectral power across key memory contrasts for eight regions of interest. A.** Delayed Recall vs. Deliberation. **B.** Delayed Recall vs. Immediate Recall. **C.** Deliberation vs. Immediate Recall. Panels **A** and **B** use matched time periods from the first five sessions of Immediate Recall and the five sessions of Delayed Recall following those first five sessions. Black-bordered regions indicated significant FDR-corrected t-tests on within subject difference scores (p < .05). Color bar corresponds to t-stat differences in panels A, B, and C. Electrodes locations corresponding to each region of interest appear on a schematic view of an electrode net (LAI,RAI: left/right anterior inferior; LSA,RAS: left/right anterior superior; LPI,RPI: left/right posterior inferior; LPS,RPS: left/right posterior superior).

Comparisons of pre-vocalization and deliberation intervals do not, however, uniquely identify the process of memory retrieval. This is because prevocalization periods also differ from deliberation in the presence of premotor activity related to the vocalization of recalled items. Switching to another recall modality, e.g., typing, would simply replace this confound with a different one. We therefore employed an immediate recall task as a control for motor activity that may confound our comparison between pre-vocalization and deliberation intervals.

Using the pre-vocalization period in our immediate-recall task as a control, we found that increased theta, decreased alpha, and increased HFA mark spontaneous (free) recall following a long delay (Figure 2B; black outlines indicate statistically-significant frequency-region pairs, that met an FDR-corrected p<0.05 threshold). This comparison recapitulates the spectral pattern observed in our comparison between long-delay recall and deliberation, but without the confound of vocalization present in Figure 2A and earlier studies. One difference, however, is that in our tighter contrast between immediate recall and long-delay recall, the retrieval related theta effect appeared to be restricted to anterior-inferior ROIs. Given the far greater demands on episodic memory retrieval in the long-delay condition, but the matched vocalization in both conditions, we interpret these biomarkers as reflecting

neural correlates of context-dependent memory retrieval. Comparisons between immediate recall and

deliberation (Figure 2C) further support this interpretation. Here we see that trying to retrieve after a

long delay (in the deliberation periods) exhibits higher HFA and low alpha-band power than during the

period immediately preceding a motor response in the immediate recall condition (black outlines

indicate statistically-significant frequency-region pairs that met an FDR corrected *p*<0.05 threshold).

Figure 3. **Time course of high-frequency activity leading up to correct recalls.** Delayed recall, immediate

recall, and delayed recall baseline log high-frequency activity (98-110 Hz power) at posterior electrodes

in the 1.0 second leading up to vocalization of recalled items, averaged for all correctly recalled items

and across subjects. Results are shown separately for phases one and two. Error bands reflect 95%

confidence computed by the method of Loftus and Masson (1994).

Because high-frequency signals provide excellent temporal resolution, we sought to examine

the timing of the increased retrieval-related HFA seen prominently in posterior ROIs. Figure 3 shows the

time course of high-frequency activity (HFA) leading up to retrieval in the long delay and immediate

recall conditions. We illustrate this time course separately for immediate recalls contributed during

phases one and two. Error bands indicate the 95% confidence interval based upon between-subject

variability in high-frequency activity. For all three conditions, HFA rose in the moments leading up to

recall, but the prevocalization HFA was highest for delayed recall, lower for phase-two immediate recall,

and lowest for phase-one immediate recall. For comparison, we indicate the baseline gamma power in

the long delay deliberation periods. This ordering of conditions aligns with the hypothesized episodic

memory retrieval demands across these conditions (such demands being highest in delayed recall, and

lowest in immediate recall when a memory test is not expected). Given that the expectation of a

subsequent test would lead to better memory encoding during phase II, as shown in Figure 1C,

mnemonic processes likely exerted a greater influence on immediate recall in phase II than in phase

one.

299   **Discussion**

Humans possess a remarkable ability to search their memory for previously experienced items

learned in a given context.   When asked to recall without the aid of specific cues, subjects generate

their own retrieval cues, based upon the context at the time of test as well as the contextual

representations evoked by recently remembered items (Kahana, 2020). Here we examined the

electrophysiological (EEG) correlates of spontaneous memory retrieval under conditions designed to

vary subjects' reliance on contextual retrieval between two extremes: In a long-delay recall condition,

we asked subjects to freely recall items not seen in at least 16 hours but encoded on previous sessions;

in an immediate recall condition, we asked subjects to read a word, pause for >1 second, and then speak

the word aloud. We chose these extreme contrasts to help distinguish pre-motor activity related to

vocalization from context-dependent memory-retrieval processes required in the long-delay task.

Contrasting immediate recall of a single word with long-delayed free recall of the entire 576-

word pool identified a spectral signature of spontaneous memory retrieval. Increased theta- and

gamma-band power (4-8 Hz and >40 Hz respectively), coupled with reduced alpha- and beta-band

power, marked periods immediately preceding recall of previously studied items. The 576 words that

subjects attempted to recall shared one essential property: namely, that they were experienced in the

context of our laboratory experiment. As such, the spectral signature of increased theta, decreased

alpha and increased gamma appears to identify a neural signature of context-dependent memory

retrieval.

Although our contrast of immediate recall and long-delay recall should reduce the influence of

premotor and electromyographic signals in comparisons between pre-vocalization and baseline periods,

we recognize that premotor activity may differ between our short- and long-delay recall tasks. Whereas

the long inter-response times in our delayed recall condition (see Figure 1e) would necessitate subjects

initializing motor commands prior to vocalization, subjects in our immediate recall task could have more

easily anticipated and maintained these motor programs. Although other differences between the

immediate- and long-delay recall conditions could also give rise to differences in neural activity,

matching for word vocalization across these conditions should provide a cleaner index of memory-

related neural activity.

Most prior EEG investigations of human memory have either compared encoding of

subsequently remembered and forgotten items (Staudigl & Hanslmayr, 2013; Klimesch, Doppelmayr,

Russegger, & Pachinger, 1996; Burke et al., 2015; Solomon et al., 2017; Hanslmayr, Spitzer, & Bäuml,

2008) or have compared successful and unsuccessful discrimination between targets and lures in a

recognition task (Jacobs, Hwang, Curran, & Kahana, 2006; van Vugt, Sekuler, Wilson, & Kahana, 2013;

Guderian & Düzel, 2005; Hsieh & Ranganath, 2014; Osipova et al., 2006). These, and other prior studies

reviewed by Herweg et al. (2020) and Hanslmayr and Staudigl (2014), report both positive and negative

correlations between theta-band power and successful mnemonic processes. In the present study we

focused on the EEG correlates of free recall, a process rarely studied using non-invasive recording

methods due to the presence of large electromyographic (EMG) artifacts caused by vocalization during

recall. By contrasting long-delayed recall with immediate recall, we find that increased theta and

decreased alpha power mark periods of episodic memory retrieval. Pastötter and Bäuml (2014) report a

similar theta-alpha pattern in a cued recall task.

Our finding that memory-related theta increases appeared at the lower bound of the theta

range aligns with several earlier reports using intracranial recordings to examine memory encoding

(Miller et al., 2018; Lega, Jacobs, & Kahana, 2012; Lin et al., 2017) as well as scalp EEG and MEG studies

of successful recognition memory (Herweg et al., 2016; Gruber, Tsivilis, Giabbiconi, & Müller, 2008).

Studies reporting negative correlations between theta and successful memory encoding or retrieval

either did not use contrasts that selected for the associative or contextual aspects of memory retrieval,

or they averaged across a broader frequency range that would include both low-frequency increases

and alpha-band decreases (see Herweg et al., 2020, for a review).

Our finding that decreased alpha band-power accompanies memory retrieval dovetails with

several recent studies. Griffiths (2019) observed decreased alpha power (and increased gamma power)

in two variants of an associative recognition task; one involving word and multi-modality stimuli and one

involving animal image cues paired with face/place images. Griffiths (2021) additionally found

decreases in alpha power during successful memory retrieval and encoding.

Simultaneous recordings of local field potentials and single neuron activity have implicated high-

frequency activity (HFA) as a correlate of neuronal firing rates (Manning, Jacobs, Fried, & Kahana, 2009).

Studying neurosurgical patients with indwelling electrodes, Burke et al (2015), Solomon et al (2017), and

Long et al. (2018) have all found greater HFA immediately preceding recall than during matched

deliberation intervals. Although invasive recordings minimize the influence of premotor artifacts, it is

still likely that some non-mnemonic factors contributed to those reported results. Our finding that high-

frequency activity increases in the moments leading up to spontaneous free recall when comparing

long-delay with immediate recall (Figure 2B) directly implicates HFA increases in the cognitive processes

involved in episodic memory retrieval.

362   The spectral methods employed in our study cannot distinguish between narrow-band

(periodic) and broadband (aperiodic) components of the EEG signal.   To determine the relative

contributions of periodic and aperiodic components, Donoghue et al (2020) introduced "fitting of

oscillations and one-over f noise," or FOOOF method. This method estimates the aperiodic (1/f)

component of the EEG signal, which is then subtracted from the original signal to estimate the periodic

components. Wen and Liu (2016) propose a different approach to decomposing the EEG signal. In

their irregular-resampling auto-spectral analysis (IRASA) method, they use mathematical properties of

the aperiodic (1/f), or fractal, component of the EEG signal to separate these from the narrowband

components. Using methods such as IRASA or FOOOF to determine the relative contributions of

periodic and aperiodic signals will likely offer additional insights into the neural basis of spontaneous

memory retrieval.

373   The present study identifies a pattern of electrophysiological biomarkers of episodic recall:

increases in frontal slow-theta (+T), and decreases in alpha-band power (-A) and increased high-

frequency, or gamma, activity with a posterior distribution (+G). These biomarkers, tag (+T-A+G) the

process of retrieval from episodic memory. They also add to an emerging body of evidence

demonstrating the utility of non-invasive methods for decoding cognitive states (Chakravarty, Chen, &

Caplan, 2020; Noh, Liao, Mollison, Curran, & de Sa, 2018; Weidemann & Kahana, 2019, 2020). Given the

ease of collecting non-invasive EEG data from human research subjects, and human's potentially unique

ability to spontaneously recall verbal items, the +T-A+G biomarker of episodic recall can serve as a basis

for future studies that investigate the role of retrieval cues, such as the temporal, semantic and spatial

contexts surrounding experienced items.

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A.

Session 1 - 5

| Practice Block | •••• | Block 1/24 | •••• | Block 8/24 | ⏲ 2 - minute break | •• | Block 9/24 | •••• | Block 16/24 | •• | ⏲ 2 - minute break | Block 17/24 | •••• | Block 24/24 |

Task Structure

IO ◆ EUROPE ···· EUROPE ◆ CLAM ···· CLAM ◆◆◆◆ 24 words
1 - 2 second pause   1 - 2 second pause

Session 6 - 10

| Delayed Recall Task | •• | Practice Block | •••• | Block 1/24 | •••• | Block 8/24 | ⏲ 2 - minute break | •• | Block 9/24 | •••• | Block 16/24 | •• | ⏲ 2 - minute break | Block 17/24 | •••• | Block 24/24 |

Delayed Free Recall Period (10 minutes)

House — Horse — Castle — Queen — King — Ocean — Dolphin ——— *interresponse time* ——— Whale

B. Percent Correct vs Block — Sessions: FIRST (red), LAST (blue)

C. Recalled Items vs Session

D. Intruded Items vs Session

E. Interresponse Time (s) vs Output Position — 40 ≤ recalls ≤ 59 (red), 60 ≤ recalls ≤ 109 (blue), 110 ≤ recalls (black)