Task-specific Aspects of Goal-directed Word Generation Identified via Simultaneous EEG–fMRI

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Abstract

■ Generating words according to a given rule relies on retrieval-related search and postretrieval control processes. Using fMRI, we recently characterized neural patterns of word generation in response to episodic, semantic, and phonemic cues by comparing free recall of wordlists, category fluency, and letter fluency [Shapira-Lichter, I., Oren, N., Jacob, Y., Gruberger, M., & Hendler, T. Portraying the unique contribution of the default mode network to internally driven mnemonic processes. *Proceedings of the National Academy of Sciences, U.S.A., 110,* 4950–4955, 2013]. Distinct selectivity for each condition was evident, representing discrete aspects of word generation-related memory retrieval. For example, the precuneus, implicated in processing spatiotemporal information, emerged as a key contributor to the episodic condition, which uniquely requires this information. Gamma band is known to play a central role in memory, and increased gamma power has been observed before word genera-

tion. Yet, gamma modulation in response to task demands has not been investigated. To capture the task-specific modulation of gamma power, we analyzed the EEG data recorded simultaneously with the aforementioned fMRI, focusing on the activity locked to and immediately preceding word articulation. Transient increases in gamma power were identified in a parietal electrode immediately before episodic and semantic word generation, however, within a different time frame relative to articulation. Gamma increases were followed by an alpha-theta decrease in the episodic condition, a gamma decrease in the semantic condition. This pattern indicates a task-specific modulation of the gamma signal corresponding to the specific demands of each word generation task. The gamma power and fMRI signal from the precuneus were correlated during the episodic condition, implying the existence of a common cognitive construct uniquely required for this task, possibly the reactivation or processing of spatiotemporal information. ■

INTRODUCTION

General consensus maintains the notion that a distributed representation of memories resides in the posterior cortical regions involved in the perception and processing of information during encoding. Various aspects of this representation are reactivated during the process of retrieval (Danker & Anderson, 2010; Damasio, 1989; James, 1890), including content (Morton et al., 2013; Gelbard-Sagiv, Mukamel, Harel, Malach, & Fried, 2008; Polyn, Natu, Cohen, & Norman, 2005), spatial (Miller, Neufang, et al., 2013), temporal (Kragel, Morton, & Polyn, 2015; Howard, Viskontas, Shankar, & Fried, 2012; Manning, Polyn, Baltuch, Litt, & Kahana, 2011), emotional (Maratos, Dolan, Morris, Henson, & Rugg, 2001), and reward (Kuhl, Shah, DuBrow, & Wagner, 2010) information. However, to what degree do task-driven demands determine which aspects of memory representations are to be recovered and represented during retrieval? It has been shown that parietal representations of a stimulus are task-independent (Harel, Kravitz, & Baker, 2014) and that task-irrelevant features of a stimulus are reactivated when a stimulus is recalled (Kuhl, Johnson, & Chun,

2013; Kuhl et al., 2010). However, under certain circumstances, parietal activity is also known to be modulated as a function of mnemonic task demands (Hutchinson, Uncapher, & Wagner, 2009; Vilberg & Rugg, 2008). Therefore, although there is some indication of the existence of such modulation in the literature, the specific role task demands may have on memory retrieval have yet to be investigated. This study thus aims to uncover and characterize the neural signature of retrieval modulations due to task demands.

To investigate how task demands affect retrieval, we compared three tasks that involve spontaneous word generation in a goal-directed manner and in accordance with a well-defined rule conveyed via a generation cue (Shapira-Lichter, Oren, Jacob, Gruberger, & Hendler, 2013). The first task consisted of the free recall of wordlists, an effective paradigm to characterize episodic memory retrieval (Miller, Lazarus, Polyn, & Kahana, 2013), that will be termed here as the episodic word generation task. The second task involved semantic fluency, which requires the generation of words from a given category—termed here as the semantic word generation task. The third task involved phonemic fluency, a task that requires the generation of words that begin with a certain letter,

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to be termed here as the phonemic word generation task. Notably, all three tasks require internal search processes, which lead to the recovery of a potential response, which in turn initiates quality control operations intended to verify suitability. The key difference between the three tasks lies in the generation cue, which targets unique information in each type of word generation. Specifically, although spatiotemporal information is the hallmark of episodic memory (Nyberg et al., 1996) and is crucial for episodic word generation, such information is irrelevant to the other word generation tasks (Dritschel, Williams, Baddeley, & Nimmo-Smith, 1992). Likewise, phonological and orthographic information is uniquely required for phonemic word generation, whereas long-term memory knowledge regarding physical and functional properties of objects, facts, and concepts is uniquely required for semantic word generation (Martin, Wiggs, Lalonde, & Mack, 1994). Comparison of the neural pattern that accompanies various types of word generation can thus unravel how task demands affect retrieval. We recently applied this approach using fMRI and found increased recruitment of posterior DMN components during the episodic condition, increased recruitment of the anterior pFC, retrosplenial cortex, and hippocampi during the semantic condition, and increased recruitment of language areas during the phonemic condition (Shapira-Lichter et al., 2013). The strongest task selectivity for episodic, semantic, and phonemic word generation was seen in the precuneus, retrosplenial cortices, and the left inferior frontal gyrus, respectively. Selectivity of regions in the parietal cortex with regards to the retrieval of episodic versus semantic information was also demonstrated with magneto-encephalography (Seibert, Hagler, & Brewer, 2011).

EEG gamma band has also been implicated in episodic (Gruber, Tsivilis, Giabbiconi, & Muller, 2008; Sederberg, Schulze-Bonhage, Madsen, Bromfield, Litt, et al., 2007; Sederberg, Schulze-Bonhage, Madsen, Bromfield, McCarthy, et al., 2007; Osipova et al., 2006; Gruber, Tsivilis, Montaldi, & Muller, 2004; Burgess & Ali, 2002; Gruber, Keil, & Muller, 2001) and semantic (Gruber & Muller, 2005; Slotnick, Moo, Kraut, Lesser, & Hart, 2002) memory. Local gamma-band oscillations have been implicated in activating neuronal representations during encoding (Donner & Siegel, 2011), with reactivation during retrieval (Zion-Golumbic, Kutas, & Bentin, 2010) and postretrieval evaluation (Johnson, Price, & Leiker, 2015), as well as in memory-related top–down reinforcement of representations (Osipova et al., 2006). Nevertheless, whether gamma activations support generic or task-specific retrieval-related processes or both have not been sufficiently addressed thus far.

Aiming to identify and characterize task-specific gamma patterns related to retrieval, we looked for distinct EEG gamma-band patterns that differentiated between word generation in response to episodic, semantic, and phonemic cues. Specifically, the EEG signals locked to and immediately preceding word articulation were compared. The logic being that articulations are the outcome of evaluation processes yielding positive evaluations of potential responses (Raaijmakers & Shiffrin, 1981), unlike periods between articulations, consisting of search cycles intermixed with postretrieval processes that yielded negative evaluations (therefore lacking an overt response). Accordingly, a constant sequence of processes related to the recovery of memory and evaluation operations is assumed to take place immediately before all word generation events, providing a platform for isolating task-specific components. Indeed, previous electrophysiological studies of free recall tasks demonstrated reactivation of both content (Morton et al., 2013) and temporal information (Manning et al., 2011), as well as increased gamma activity (Burke et al., 2014; Sederberg, Schulze-Bonhage, Madsen, Bromfield, Litt, et al., 2007) immediately before word articulation. Yet none of these studies specifically targeted the task demand modulation of the signal. Critically, whereas the processes that precede articulation in the present paradigm vary as a function of the cue, preparation and execution of articulation are similar across all tasks. Thus, comparisons between tasks will cancel out the articulation-related components, revealing the unique manifestation of each word generation task. We hypothesized that the specific demands of each type of word generation would produce unique patterns of gamma-band activity immediately before word articulation. Notably, task specificity could appear in the spatial and/or temporal dimension, in the responsiveness of specific electrodes and/or the distinct timing of the response.

Over the past decades, a great research effort was invested in characterizing memory retrieval using both electrophysiological and neuroimaging techniques, gaining significant insights on both fronts. Integrating the knowledge and principals achieved by these two complementary methods would be advantageous. Accordingly, in this study, we further aimed to characterize the relation between the putative task-specific retrieval-related gamma patterns and the task-specific fMRI signals. To this end, we examined the EEG activity recorded simultaneously with the fMRI data described above, the results of which were reported in full length in Shapira-Lichter et al. (2013). A relation between gamma bands and fMRI BOLD signals has been repeatedly shown in animal (Goense & Logothetis, 2008) and human (Mukamel et al., 2005) studies, including simultaneous fMRI–EEG studies (Scheeringa et al., 2011; Mulert et al., 2010). On the basis of this well-established relationship, we hypothesize that a positive correlation will be found between the word generation task-specific gamma-band and fMRI manifestations.

METHODS

Procedure

Eighteen participants (mean age = 27 years, SD = 5.7 years; nine men and nine women; mean = 14.4 years of education,

SD = 2.81 years) performed a block design word generation task during simultaneous fMRI–EEG recording. The task consisted of three conditions: (i) episodic free recall, in which participants freely recalled words from previously studied word lists (see details below); (ii) semantic fluency, in which participants generated exemplars belonging to a certain semantic category; and (iii) phonemic fluency, in which participants generated words beginning with a certain letter. Regardless of condition, a single generation cue (i.e., a certain category/letter/episodic cue, see below) was visually presented throughout the entire 18-sec block, and participants were instructed to generate as many words as possible with cues chosen to prevent ceiling effects. A total of 21 word generation blocks with six to eight blocks of each of the three word generation conditions were presented. The order of the word generation conditions was pseudorandom and fixed across participants, whereas the order of the specific cues was randomly assigned for each participant. Task blocks were separated by 6- to 9-sec periods of visual fixation (see additional details in Shapira-Lichter et al., 2013). Paricipants' verbal responses were recorded via an MR-compatible noise reduction audio system (Optoacoustics Ltd., Moshav Mazor, Israel) and analyzed offline using Audacity software.

As mentioned above, episodic word generation required free recall of previously studied word lists acquired as part of another paradigm. This paradigm involved three cycles of learning and free recall of word lists followed by a recognition test that consisted of both target and distracting words. A single word list was studied during a prescan practice session, and three additional word lists were presented during the fMRI scan (for additional details, see Shapira-Lichter et al., 2012). Episodic generation in the current study thus consisted of three types of blocks: retrieval of words learned during practice, retrieval of words learned during scanning, and retrieval of distracting words from the recognition test.

EEG Acquisition

Continuous EEG data were recorded simultaneously with fMRI while participants performed the word generation task. EEG was collected using an MR-compatible system, including a BrainAmp-MR EEG amplifier connected to a 32-channel electrode cap with sintered Ag/AgCl ring electrodes and one ECG channel attached to the back (Brain Products, Munich, Germany). The reference electrode was placed between Fz and Cz. Impedance was kept below 15kΩ. Raw EEG was sampled at 5 kHz and recorded using Brain Vision Recorder software (Brain Products).

EEG Data Analysis

Because we aimed to study retrieval and postretrieval operations that take place immediately before overt respond-

ing and to avoid noise effects associated with articulation, only EEG activity that preceded word generation was analyzed (excluding motor preparation signals). Therefore, the analyses focused on a window of 1000–450 msec before articulation onset (see details below). The window was set to start 1000 msec before articulation because a reinstatement of category-specific patterns was shown to peak around 1000 msec before articulation onset (Morton et al., 2013) and because, as the analyzed time window increased, the number of events available for analysis decreased, as the length of the time window dictates the minimal ISI (see details below). Consistent with previous studies, the last segment of up to a few hundred milliseconds before articulation was discarded from analysis (Morton et al., 2013). This is due to motor effects, which are known to strongly affect the signal (Porcaro, Medaglia, & Krott, 2015), a phenomena that was also evident in our data; visual inspection indicated many trials in which this segment included speech-like noise (described in the fourth preprocessing step, see details below). The beginning of each word articulation was manually identified in the audio recording and inserted as an EEG event. Words in which the gap between the start of the articulation and the start of the previous articulation was less than 1500 msec were discarded from analysis, because such small gaps did not allow sufficient separation between consecutive responses. EEG data analysis was performed offline with MATLAB software (The MathWorks, Natick, MA) and EEGLAB 12.0.2.4b software package (Delorme & Makeig, 2004). The data were preprocessed as follows: (i) MR gradient artifacts were removed using FMRIB plug-in for EEGLAB and a FASTR algorithm (University of Oxford Centre for Functional MRI of the Brain; Iannetti et al., 2005; Niazy, Beckmann, Iannetti, Brady, & Smith, 2005); (ii) EEG data were downsampled to 250 Hz; (iii) cardioballistic artifacts were removed using the same plug-in, with an optimal basis sets approach (Christov, 2004; Kim, Yoon, & Park, 2004); and (iv) cleaning of speech segments, because speech in the scanner may cause large movement artifacts that interfered with the subsequent independent component analysis (ICA) of the EEG data. Notably, the cleaning procedure was employed only to mark and remove articulation-related noise segments from the EEG data that would possibly interfere with the ICA. The remaining data set did not undergo any other manipulation as part of our procedure. Also, the procedure was not intended or used to mark retrieval times—those were encoded manually based on the audio recordings of the word generation. The cleaning procedure was applied as follows: Each participant's speech-related EEG profile was identified, and epochs with similar profiles were marked for cleaning. Identification of speech-related signals was done using the word list learning and recall task described above (Shapira-Lichter et al., 2012). Specifically, the EEG response to epochs known to include speech was compared with epochs known to be silent. Epochs with speech consisted of periods in which participants pronounced the sound "beep" in response to a tone; intervals

of 1.4 sec, which began 0.2 sec before the sounding of a tone. Silent epochs consisted of the same interval lengths before and after instruction trials. Speech identification involved the following steps: (a) For each electrode and condition (speech and silent), a fast Fourier transform was applied, and the average power between 1 and 30 Hz was computed. (b) The difference in power between the two conditions was computed, and the upper 20% of the difference between scores was identified. (c) Identification of the six electrodes with the largest difference scores along with the frequency range of each of these electrodes was documented and considered to represent the speech profile for each participant. The choice of six electrodes roughly corresponds with the electrodes scattered along the perimeter of the head (Electrodes 11, 12, 13, 14, 29, 30), which are most prone to capture speech artifacts related to muscle activity and artifacts related to articulation movements in the magnetic field. Indeed, these electrodes were identified as speech-related in most participants: Electrodes 29 and 30 were selected as part of the six electrodes in 11 of 14 participants (each), Electrodes 11 and 14 in 12 of 14 participants (each), and Electrodes 12 and 13 in 13 of 14 participants (each). The identified profile was then applied to "clean" the data in the word generation paradigm performed by the participant. This procedure involved the following steps: (a) A time–frequency Stockwell transform was employed across the whole data set. (b) In the identified six electrodes, the averaged power in the identified frequency range of each electrode was computed and averaged across the six electrodes. (c) The time segments in which this measure obtained the top 10% values were considered to represent the speech periods. Examination of the top 10% of the values is based on the approximated relative amount of time speech occurred out of the entire length of the experiment. (d) The data in all electrodes were then zeroed in the identified time segments, along with a smoothing of 0.5 sec. As stated above, the procedure was used only to remove articulation noise segments from the data, preparing it for ICA. (e) Artifacts caused by blinks, eye movements, and residuals from cardioballistic artifacts were removed from the EEG recording using ICA. Artifacts were distinguished from brain activity based on inspection of the time course of the components and their projection to scalp electrode sites. Eye blink component time courses usually have brief large monopolar peaks and project most strongly to frontal sites, showing a high correlation with the frontal electrodes (FP1, FP2). Similarly, components with cardioballistic artifact residuals have a high correlation with the ECG channel. Artifact removal of components with one of the above characteristics was done by subtracting the relevant independent component from the original EEG recording (Li & Principe, 2006). Thus, ICA was only used for the removal of residual cardiobalistic artifacts and blinks. At this stage, the quality of the EEG data in 3 of 18 participants was insufficient, yielding a cohort of 15 participants.

Event-related Spectral Perturbation Analysis

Following preprocessing, the signal was segmented into an interval beginning 1000 msec before and ending 100 msec after the onset of articulation. For each epoch, baseline correction was performed by subtracting the average of the signal in a time window of 1000–450 msec before the onset of articulation. Visual inspection was used to remove trials with extremely high and/or sharp amplitudes and trials marked as speech-related signals in the relevant range. A minimum of 12 events per condition was confirmed for all but one participant who had only six events in the episodic word generation condition. This participant was discarded from all further analyses, yielding a final cohort of 14 participants. Event-related spectral perturbation (ERSP) was computed for each participant, electrode, and experimental condition, for each trial with a short-time Fourier transform with a fast Fourier transform padding of 16, frequency range of 3–70, and logarithmic scale of power in dB. An averaged baseline power of $(-1000) - (-450)$ msec was used for the normalization of power for each trial. Repeated-measures ANOVA (rm-ANOVA) was used to identify the best condition-distinguishing electrode(s). All three conditions were compared across participants, examining the average power in the low (30–50 Hz) and high (50–80 Hz) gamma bands separately. Intervals of 100 msec were used, creating three time windows: 800–700 msec, 700–600 msec, and 600–500 msec before articulation ($p < .05$, FDR correction for multiple comparisons, permutation with 5000 iterations). This analysis was followed by spectral analysis within the identified electrodes using a short-time Fourier transform. ERSPs of the various conditions were compared using an rm-ANOVA ($p < .025$, permutation, 5000 iterations), creating a significance matrix that indicates within which times and frequencies the three conditions differed. Subsequent analyses were conducted only on large clusters (>200 cells in the significance matrix). The average power for each time–frequency cluster of every condition was extracted per participant, and post hoc pairwise comparisons between all possible pairs of conditions ($p < .05$, Bonferroni correction) were conducted to identify the distinguishing conditions. For each time–frequency cluster identified as task-specific, Pearson correlations with a Bonferroni correction were used to evaluate the dependency between the signal change in that cluster and the signal change in the following cluster that emerged in that condition (see details in the Results section).

fMRI–EEG Correlation Analysis

In a recent article, we presented the brain regions selectively associated with each of the word fluency conditions based on simultaneous fMRI–EEG (Shapira-Lichter et al., 2013). The current work describes the EEG data recorded simultaneously and its relation to the fMRI results presented in the previous article. Although a number of

regions contributed to episodic or semantic fluency, we had to limit the analysis to a few prudently predefined ROIs, owing to the small sample size and the weak effect it may yield. Accordingly, only the regions that showed the greatest contribution to each type of word generation were examined in this study. Specifically, the strongest selectivity for the episodic condition, as compared with semantic and phonemic conditions (episodic > semantic and phonemic blocks), was seen in the precuneus (peak Talairach coordinates: $-4 -75\ 42$, $t = 11.7170$, $p = .0000$, n of voxels 20,811). The strongest selectivity for the semantic condition (semantic > episodic and phonemic blocks) was observed in the retrosplenial cortex (peak Talairach coordinates: $-7 -56\ 12$, $t = 9.2532$, $p = .0000$, n of voxels = 1068; for a full list of all regions and values, see Table S2 in Shapira-Lichter et al., 2013). In this study, ROIs were defined around these peaks using a Gaussian mask with a 3-mm radius (Figure 3A). Preprocessing and processing parameters were identical to those used in the previous analysis of the data described above (see Shapira-Lichter et al., 2013). Consistent with the previous analysis, only blocks with balanced performance levels across all three conditions were included in the fMRI analysis (for a detailed description of the balancing procedure, see Shapira-Lichter et al., 2013). Performance could not be balanced for one participant who was thus excluded from the fMRI–EEG correlation analysis. The difference in percent signal change (%SC) from baseline in the fMRI data of each participant and ROI was computed and compared between the condition for which that ROI was selective and the average of the other two conditions (i.e., in the precuneus: episodic minus the average of the semantic and phonemic blocks, in the retrosplenial cortex: semantic minus average of episodic and phonemic blocks). These %SC indices will be referred to as episodic-%SC and semantic-%SC, respectively. Similarly, in each EEG time–frequency cluster, the difference in averaged power between the condition of interest and the two other conditions was computed for each participant. This approach was taken to compensate for nonspecific interindividual differences. These indices were thus termed episodic-EEG and semantic-EEG, respectively. Pearson correlations were calculated for the corresponding fMRI and EEG indices, yielding two "original" correlations: one between episodic-%SC from the precuneus and episodic-EEG and another between semantic-%SC from the retrosplenial and semantic-EEG. The specificity of these "original" correlations was determined by examining whether they were significantly larger than "alternative" correlations (see full details in the Results section). Correction for multiple comparisons was conducted using a Bonferroni correction, dividing the p value by the number of "original" and "alternative" correlations. The relationship between each "original" and "alternative" correlation could be of two types: (1) nonoverlapping—each calculated on two nonoverlapping sets of variables, with all variables derived from the same sample—using the Raghunathan, Rosenthal, and Rubin's z test (Uitenbroek, 1997), or (2) overlapping—a common variable for both conditions was computed by the asymptotic covariance of the estimates (Steiger, 1980) and using the asymptotic z test (Lee & Preacher, 2013).

RESULTS

Behavioral Results

Before data cleaning, an average of 6.3 responses per block were generated in the phonemic condition, 6.9 responses in the semantic condition, and 5.2 responses in the episodic condition (one-way rm-ANOVA with three levels: phonemic condition, semantic condition, and episodic condition, $F(2, 26) = 8.696$, $p < .001$). The balancing procedure that was applied to the fMRI data led to similar performance levels in the three experimental conditions, with an average of 6.45, 6.7, and 6.52 responses in the phonemic, semantic, and episodic conditions, respectively ($F(2, 26) = 0.413$, $p = .666$). Following the EEG cleaning procedures, the average total number of words generated in each word generation task was 17.4 words in the episodic condition (range = 12–30), 18.3 words in the semantic condition (range = 13–25), and 27.6 words in the phonemic condition (range = 18–34). This indicates a minimum of 12 events per condition for each participant. In terms of ISIs (the time intervals between the beginning of word articulation), the conditions differed in average ISIs both before EEG cleaning procedures were implemented, when examining the entire data set ($F(2, 26) = 8.579$, $p < .001$; averaged ISI for the phonemic, semantic, and episodic conditions: 2.6, 2.1, and 2.2 sec, respectively), and after EEG cleaning ($F(2, 26) = 5.812$, $p < .008$; averaged ISI for the phonemic, semantic, and episodic conditions: 3.1, 3.2, and 3.6 sec, respectively). Nevertheless, because this study only focuses on the period that immediately precedes articulation, minimal length differences of longer ISIs are unlikely to affect our results. In contrast, articulations that follow a short ISI may include residual effects from the preceding word. Remarkably, the proportion of short ISIs (i.e., ISIs between 1.5 and 2 sec in length) in the final EEG data set did not differ across the three experimental conditions ($F(2, 26) = 1.117$, $p = .34$; averaged percent of short ISI in the phonemic, semantic, and episodic conditions: 0.19, 0.13, and 0.17, respectively).

EEG Results

rm-ANOVA ($n = 14$, permutation, 5000 iterations, $p < .05$, FDR-corrected) was used to identify electrodes in which the EEG signal distinguished between the episodic, semantic, and phonemic word generation conditions immediately before word generation. This analysis was conducted once on the low gamma band (30–50 Hz) and once on the high gamma band (50–80 Hz). For the high gamma band, none of the electrodes distinguished between the
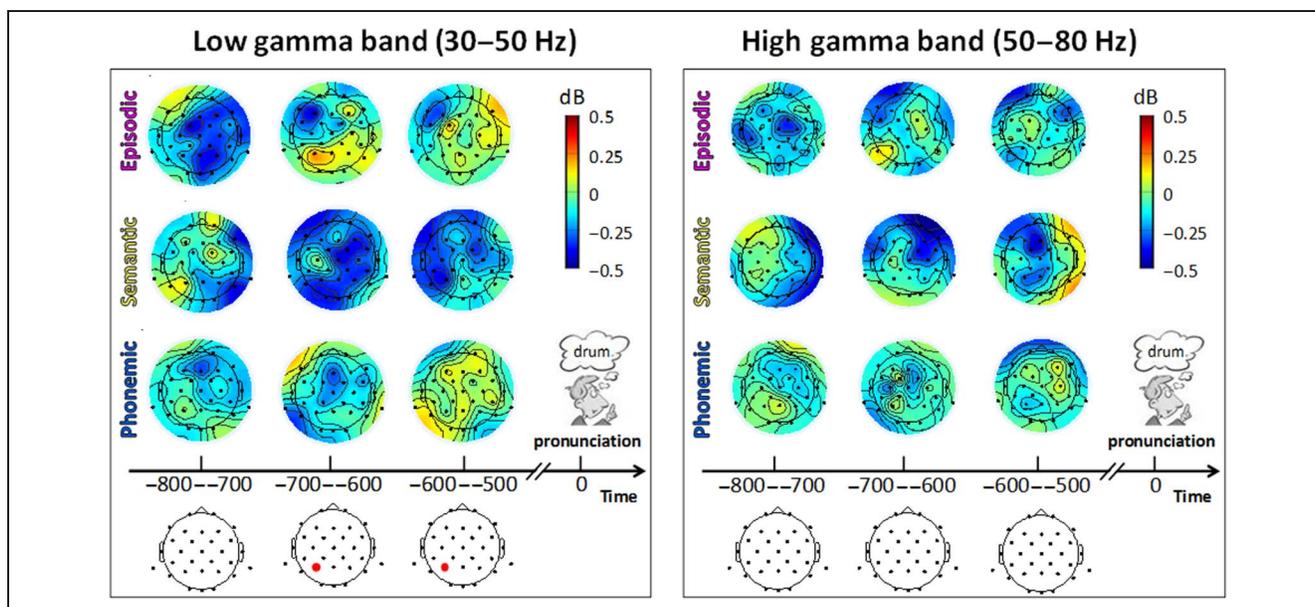
Figure 1. Spatial distribution of gamma dynamics preceding word generation. Scalp plots of low gamma band (30–50 Hz) and high gamma band (50–80 Hz) power were computed using 100-msec bins. An rm-ANOVA was used to identify electrodes that significantly distinguish the three word generation conditions (bottom of figure), revealing electrode P3 for the low gamma band. $N = 14$, permutation (5000 iterations), $p < .05$, FDR-corrected.

three-generation conditions (Figure 1, bottom right). For the low gamma band, electrode P3 emerged as a strong distinguishing electrode between the three conditions (Figure 1, bottom left) and was thus chosen for subsequent analyses. Spectral analysis was conducted on this electrode using ERSP analysis (Delorme & Makeig, 2004; Makeig, 1993; Figure 2, $p < .025$, permutation, 5000 iter-

ations). This analysis revealed three major time–frequency clusters in which the three conditions differed (Figure 2B). Post hoc pairwise comparisons were conducted within each of these three time–frequency clusters. Specifically, all pairs of word generation conditions were compared using the power of each participant per condition, averaged across all time points within that time–frequency
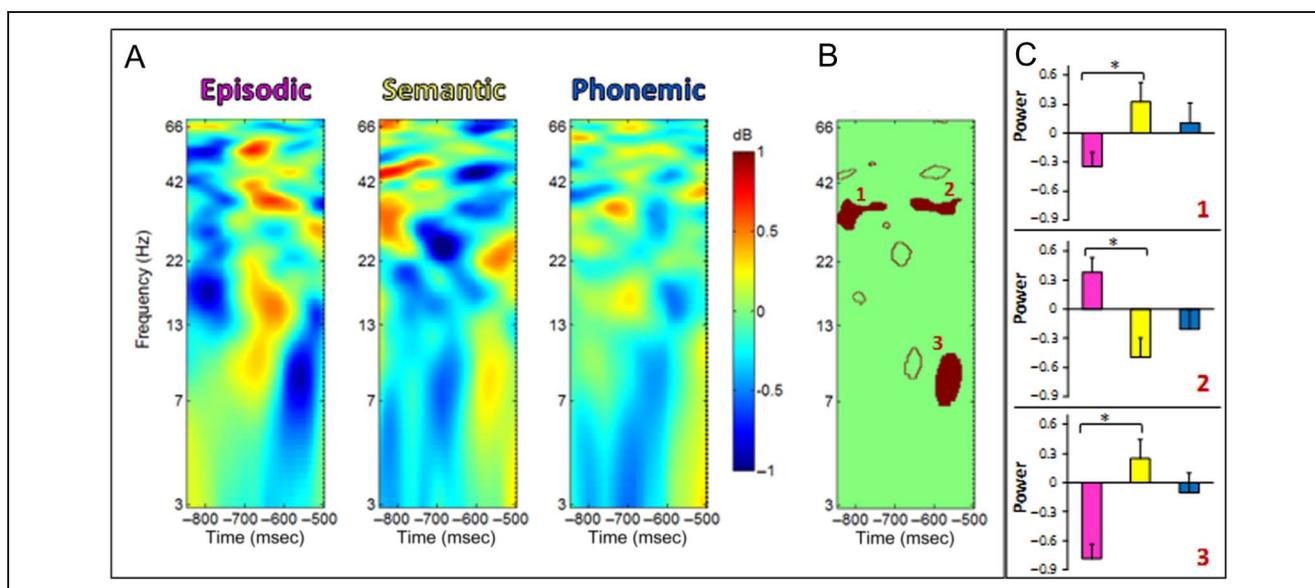

Figure 2. Spectral analysis of activity preceding word generation in electrode P3. ERSP plots showing mean changes in spectral power immediately before word generation relative to baseline (A). rm-ANOVA was used to identify times/frequencies in which the three word generation conditions differed (B). Clusters larger than 200 cells in the significance matrix are marked in solid red, whereas smaller clusters (not analyzed) are marked with a red outline. $N = 14$, $p < .025$, permutation (5000 iterations). Bar plots (C) present the average power in each condition (episodic in pink, semantic in yellow, phonemic in blue) in each time–frequency cluster identified by the rm-ANOVA. *Significant differences identified in post hoc comparisons ($p < .05$, Bonferroni-corrected).

cluster ($p < .05$, Bonferroni-corrected, dividing the p value by the 9 comparisons conducted: 3 clusters by 3 condition pairs). The results indicate a significant difference between the episodic and semantic conditions for all time–frequency clusters ($t(13) = -4.6$, $p < .01$; $t(13) = 5.3$, $p < .01$; $t(13) = -3.36$, $p < .03$, for the first, second, and third cluster, respectively; Figure 2C). The semantic and phonemic conditions and the episodic and phonemic conditions did not differ for any of the clusters. Taken together, these findings show a main difference between the episodic and semantic conditions. Indeed, these conditions had opposite patterns in the identified times/frequencies (Figure 2A). In the episodic condition, there was a transient decrease in low gamma power, about ~800 msec before episodic generation, followed by a transient increase in the low gamma band, at ~650 msec, with a decrease in high theta/low alpha power shortly afterwards. The opposite pattern was seen in the semantic condition, manifested as an increase in the low gamma band ~800 msec before semantic generation, followed by a decrease in the low gamma band ~650 msec before semantic generation, with an increase in the theta–alpha band shortly afterwards. Thus, subsequent analyses focused on the episodic and semantic conditions, later to be referred to as conditions of interest.

Next, we examined the robustness of the pattern of transient electrophysiological changes preceding episodic and semantic generation in electrode P3. In each of the identified time–frequency clusters, each participant's average power in the condition of interest was normalized by subtracting the average power of the two other conditions (i.e., subtracting common aspects of word generation not specific to the condition of interest). This analysis revealed the substantial robustness of the EEG patterns. Eighty-six percent of the participants showed a relative increase in low gamma power ~800 msec before semantic generation (mean difference = 0.45 dB). In addition, 86% of the participants showed a relative increase in the low gamma band ~650 msec before episodic generation (mean difference = 0.74 dB). Furthermore, 86% of the participants showed a relative decrease in the low gamma band ~650 msec before semantic generation (mean difference = −0.58 dB), and 79% of the participants showed a decrease in theta–alpha power ~550 msec before episodic generation (mean difference = −0.85 dB; see individual scores in Table 1).

Table 1. Individual Participant Activity Patterns in Electrode P3

| Participant | Cluster 1 | Cluster 2 | | Cluster 3 |
	SF vs. EF & PF	EF vs. SF & PF	SF vs. EF & PF	EF vs. SF & PF
1	1.29	0.97	−0.73	−1.12
2	−0.45	−0.48	0.43	0.20
3	0.81	0.80	−0.26	−0.12
4	0.58	0.59	−0.97	−1.22
5	0.18	0.77	−0.69	−1.97
6	0.72	2.25	−0.36	−1.90
7	0.48	−0.02	−0.59	−0.79
8	0.23	1.88	−0.26	−1.70
9	0.84	0.63	−0.99	−0.77
10	0.23	0.82	−1.06	−0.81
11	−0.01	0.57	0.31	0.96
12	0.91	0.32	−1.24	−1.15
13	0.09	0.10	−0.57	−1.92
14	0.38	1.12	−1.19	0.35
Average	0.45	0.74	−0.58	−0.85
% Pattern	0.86%	0.86%	0.86%	0.79%

The averaged power difference in the time–frequency clusters identified by an rm-ANOVA as differentiating the three word generation conditions (see Figure 2). Scores are calculated as the difference in mean power between the condition of interest and the mean power in the two other conditions. Results indicate that the vast majority of participants (79–86%) show the pattern identified at the group level. That is, a selective increase in the low gamma band ~800 msec before semantic generation (Cluster 1 in Figure 2); a selective increase in the low gamma band ~650 msec before episodic generation and a selective decrease in the same band and at the same time before semantic generation (Cluster 2 in Figure 2); and a selective decrease in the theta–alpha band ~550 msec before episodic generation (Cluster 3 in Figure 2).

SF = semantic fluency; EF = episodic fluency; PF = phonemic fluency.

We then assessed whether there was a relation within each condition between the gamma increases and the electrophysiological change that followed. A Pearson correlation was computed once for the episodic and once for the semantic condition. In the episodic condition, a correlation was calculated for the power of the low gamma band at ~650 msec before generation (Blob 2 in Figure 2) and the power of the high theta–low alpha bands that followed (Blob 3 in Figure 2). This yielded a significant negative correlation ($r_{(14)} = .62$, $p < .05$, two-tailed, Bonferroni-corrected, dividing the p value by the 2 comparisons conducted), implying that both changes in power are related to one another. In the semantic condition, a correlation was calculated for the increase in gamma power (Blob 1 in Figure 2) and the decrease in gamma power that followed (blob 2 in Figure 2). This correlation was not found to be significant ($r_{(14)} = .04$, $p < .9$, two-tailed).

Correlation with the fMRI Data

We next examined the relation between the task-specific electrophysiological patterns of modulated gamma power and the task-specific changes in the BOLD signal. For both fMRI and EEG signals, each condition of interest was normalized by the two other conditions, subtracting their averaged %SC (fMRI data) or averaged power (EEG data). fMRI ROIs were defined by the results obtained in our previously published article (see Figure 3, top left in Shapira-Lichter et al., 2013). Briefly, the activity (calculated as the amplitude averaged across the entire 18-sec blocks)

of each condition, from this whole-brain analysis, was compared with the two other conditions. This revealed brain regions selectively contributing to each of the word fluency tasks. The strongest peaks of activation during the episodic and semantic conditions were seen in the precuneus and retrosplenial cortex, respectively (see Shapira-Lichter et al., 2013). The ROIs for this study were thus selected around these peaks (see Methods section). We first confirmed that the task-selective response of the BOLD signal that emerged in the original whole-brain analysis was maintained when sampled around peak of activation. In other words, we confirmed that the ROIs, as defined for the current study, conserve their selectivity property indicated in the previous study. In both ROIs, the averaged percent signal change in the condition of interest was significantly different from the other conditions (precuneus: $t(12) = 5.26$, $p < .001$; retrosplenial cortex: $t(12) = 3.42$, $p < .005$; Figure 2, bottom left).

We then calculated the correlations between the BOLD and EEG signals, using the index of %SC from the relevant ROI and the index of increase in gamma band from the relevant time–frequency cluster for each experimental condition. A Pearson correlation was first computed for the semantic-%SC in the retrosplenial cortex and semantic-EEG power in Cluster 1 (i.e., in the ~800 msec before articulation; scores were normalized, see details in Methods section). This correlation was nonsignificant ($r_{(13)} = -.26$, $p < .97$, one-tailed, Bonferroni-corrected). A Pearson correlation was then computed for the episodic-%SC in the precuneus and episodic-EEG power in Cluster 2 (i.e., in the ~650 msec before articulation; to be referred to

Figure 3. Correlations between fMRI and EEG signals. (A) Selectivity to the word fluency tasks was identified by comparing the BOLD fMRI signal of entire word fluency blocks. Each condition was compared with the other two conditions (see methodology and result details in Figure 2 and Table S2 in Shapira-Lichter et al., 2013). ROIs presented in the top panel were defined using a Gaussian mask with a 3-mm radius around the strongest peaks of activation obtained in each selectivity contrast. The greatest selectivity for the episodic condition (identified by the contrast
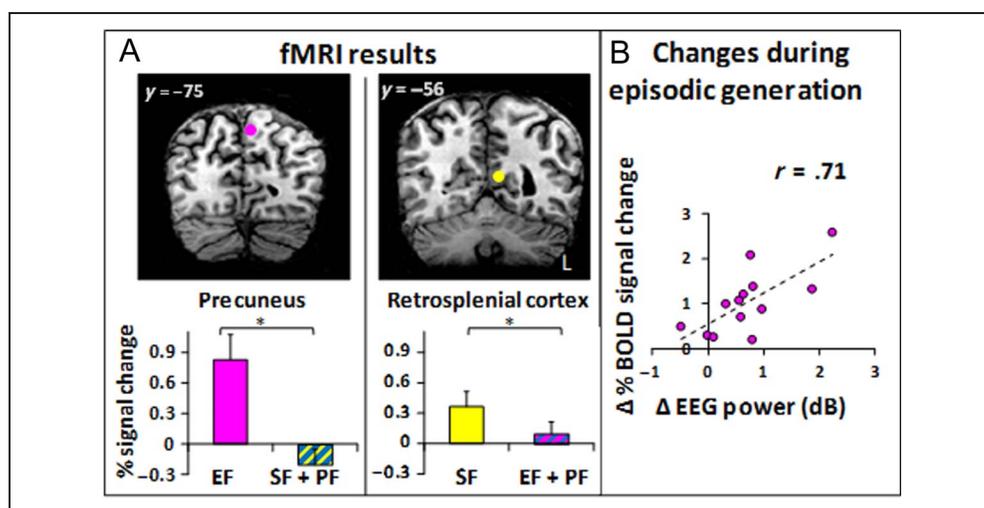
episodic > semantic plus phonemic blocks) was found in the Precuneus (peak Talairach coordinates: −4 −75 42). The greatest selectivity for the semantic condition (identified by the contrast semantic > episodic plus phonemic blocks) was found in the retrosplenial cortex (peak Talairach coordinates: −7 −56 12). Bar plots at the bottom show average percent signal changes from baseline (fixation) in the condition to which that region was selective, as compared with the two other conditions (mean ± SE). *Significant differences identified by paired t tests ($p < .005$). (B) Pearson correlation between the difference in BOLD percent signal change in the precuneus during episodic blocks versus semantic and phonemic blocks (episodic minus the average semantic and phonemic) and the difference in average power in the gamma band ~650 msec (Cluster 2 in Figure 2) before word generation, between episodic generation versus semantic and phonemic generation (episodic minus the average semantic and phonemic). $r_{(13)} = .714$, $p < .05$ (Bonferroni-corrected), one-tailed. The larger the increase in EEG power ~650 msec before episodic generation, the larger the increase in activity in the precuneus during episodic blocks.

as "episodic correlation"). This correlation was found to be significant ($r_{(13)} = .714$, $p < .015$, one-tailed, Bonferroni-corrected). Nevertheless, this finding may be the result of nonspecific relations between BOLD and EEG signals. For one, it is possible that the BOLD signal in the precuneus might be related to a gamma power increase regardless of the task. Two analyses were conducted to preclude this possibility. First, we calculated the correlation between semantic-%SC in the precuneus and semantic-EEG power in Cluster 1 (the cluster that demonstrated gamma increase in the semantic condition). Importantly, this correlation was not significant ($r_{(13)} = -.05$, $p < .99$, one-tailed, Bonferroni-corrected) and was significantly smaller than the "episodic correlation" (Raghunathan, Rosenthal, & Rubin's test $Z = 1.8505$, $p < .0131$, one-tailed, uncorrected). Second, we calculated the correlation between semantic-%SC in the precuneus and semantic-EEG power in Cluster 2. This correlation was also not significant ($r_{(13)} = .029$, $p < .825$, one-tailed, Bonferroni-corrected) and was marginally smaller than the "episodic correlation" (Raghunathan, Rosenthal, & Rubin's test $Z = 1.313$, $p = .0734$, one-tailed, uncorrected). Nonspecific BOLD–EEG signal relations could also occur if gamma power increases in Cluster 2 (the cluster that demonstrated gamma increases in the episodic condition) during episodic word generation was related to BOLD signals in various brain areas and not only the precuneus. To rule out this possibility, we calculated the correlation between episodic-%SC in the RSC and episodic-EEG power in Cluster 2. This correlation was nonsignificant ($r_{(13)} = -0.55$, $p < .135$, one-tailed, Bonferroni-corrected) and again was significantly smaller than the "episodic correlation" ($z = 3.274$, $p < .00053$, one-tailed, uncorrected). These results support the conclusion that the relation between BOLD and EEG signals is unique to the combination of episodic memory; BOLD increases in the precuneus, and gamma power increases in Cluster 2.

DISCUSSION

Episodic and semantic word generation was preceded by a specific electrophysiological pattern found in the left parietal electrode P3. Yet in each condition, it occurred at different periods in time (Figures 1 and 2). In the episodic condition, this pattern consisted of a transient increase in low gamma power ~650 msec before word articulation and immediately followed by a decrease in the high theta–low alpha band. A similar increase in gamma power was seen in the same electrode ~800 msec before semantic word generation (Figure 2), yet in this case, it was followed by a decrease in gamma power. This profile was also evident at the individual level (Table 1). These findings indicate a task-specific modulation of the gamma-band signal that is related to word generation. As all tasks involved a similar degree of articulation, the modulation must be derived by the unique demands of each type of word generation.

The task-specific patterns possibly reflect top–down modulation of memory representations as a function of task demands. Two lines of evidence support this claim. First, although scalp EEG does not allow for unequivocal inferences of the neural generators of a certain signal, the location of the effect in electrode P3 anatomically fits the left posterior parietal cortex. This region has been implicated in top–down attention processing of episodic memory (Hutchinson et al., 2009) and in modulating the accessibility of memory representations during effortful retrieval, making task-specific information more salient (Mecklinger, 2010). In the same vein, the intraparietal sulcus was also implicated in representing task-sensitive contexts that support control mechanisms (Waskom, Kumaran, Gordon, Rissman, & Wagner, 2014). Second, gamma activity has been attributed to memory-related top–down reinforcement of representations (Osipova et al., 2006).

Particularly, the transient increase in gamma power seen before either episodic or semantic word generation may be related to processing temporal–spatial features of the generated word. This assertion is based on the well-accepted centrality of temporal and spatial information in episodic memory in general (Nyberg et al., 1996), as well as on the particular implementation of the episodic condition in this study. That is, generating words in the episodic condition required retrieval of recently tagged words, while distinguishing words that were tagged during the practice and scan sessions, relying on precise spatial (task location: practice-room/scanner) and/or temporal (task timing: before/during scan) mnemonic details (see Methods section). Identification of P3 as the electrode that best distinguished between the three word generation tasks (Figure 1) and the episodic and semantic conditions (post hoc comparisons, Figure 2B) support this interpretation. Selectivity of the left posterior parietal cortex for episodic versus semantic tasks has been observed (Shapira-Lichter et al., 2013; Seibert et al., 2011). The correlation between the increase in gamma power in electrode P3 and the increase in the BOLD signal in the precuneus (Figure 3B) is also consistent with the spatiotemporal interpretation. Previous studies showed that increased precuneus activity (Ekstrom, Copara, Isham, Wang, & Yonelinas, 2011; Mayes, Montaldi, Spencer, & Roberts, 2004) and its functional connectivity with the hippocampi (Zhang & Ekstrom, 2013) and parahippocampal gyrus (Watrous, Tandon, Conner, Pieters, & Ekstrom, 2013) are related to spatial information retrieval. Thus, the increased gamma power observed in this study, which correlated with precuneus activity, may also reflect the processing of spatial and/or temporal information. Additional support of this interpretation is presented in a study that found increases in posterior gamma power during a spatial working memory task (Jokisch & Jensen, 2007). The present finding extends this relation to the domain of declarative memory.

Intriguingly, the transient increase in gamma power in electrode P3 was seen only when the word was generated from declarative memory (i.e., episodic and semantic

word generation) but not during phonemic word generation. Utilizing this spatiotemporal interpretation, the difference in the timing at which the gamma increase occurred may be attributed to the difference in the task relevance of the spatiotemporal information within the two tasks: Although this information is critical and probably comprises the final stage of verification in the episodic condition, it is irrelevant and even distracting in the semantic condition (Dritschel et al., 1992). In the episodic condition, the increase in gamma power was immediately followed by suppression of low-frequency activity, a pattern that is often reported (Donner & Siegel, 2011). Moreover, these activity changes were negatively correlated, implying a contribution to related processes. Notably, low alpha-band desynchronization is thought to reflect enhanced cortical and mental activation (Pfurtscheller, 2003; Rugg & Allan, 2000); thus, the decrease in high theta–low alpha power is in the same direction as the increase in gamma power. The decrease in high theta–low alpha for episodic word generation possibly reflects an additional processing of the spatiotemporal information in the experimental condition for which it was relevant. Several lines of evidence support this notion; modulation in the alpha–theta bands during memory tasks has been attributed to the selective utilization of stimuli-related semantic information when found to be beneficial to performance (Zion-Golumbic et al., 2010). Likewise, alpha oscillations were implicated in information-specific processing, with decreased alpha power suggested to activate mnemonic representations of specific features. Particularly, retrieval of spatial information was shown to be mostly associated with parietal activation (Khader & Rosler, 2011). This finding especially attests to the attribution of high theta–low alpha decreases in the processing of task-relevant spatiotemporal information during episodic word generation. Thus, the increase in gamma power and the following decrease in high theta–low alpha power that correlated with it presumably reflect the recovery or processing of task-relevant spatiotemporal information, with articulation occurring shortly afterward.

Considering this spatiotemporal interpretation, a key question is why a similar increase in gamma power is present before semantic word generation, given that spatiotemporal information does not aid this task (Dritschel et al., 1992). Previous studies showed reactivation of task-irrelevant features of a stimulus when the stimulus is recalled (Kuhl et al., 2013). This phenomenon was also demonstrated in the specific context of word generation tasks (Perret, 1974). For example, semantic features have been shown to automatically affect phonemic word generation (e.g., Sung, Gordon, Yang, & Schretlen, 2013). A related question refers to the restriction of the transient increase in gamma power to the episodic and semantic conditions, as such an increase was not seen for phonemic word generation. Great similarity and interdependence between the two types of declarative memory, namely, the episodic and semantic conditions, have been acknowl-

edged (Greenberg & Verfaellie, 2010). Hence, there is possibly a general tendency to automatically represent spatiotemporal features during declarative memory retrieval, regardless of task demands. It is further possible that the representation of spatiotemporal features during the semantic task stems from the specific experimental context of this study. That is to say, the inclusion of an episodic memory condition may have affected the processes and patterns related to semantic memory. Alternatively, recovery of spatiotemporal information during semantic word generation may result from the reliance on mental imagery of concrete autobiographic episodes as a retrieval strategy to aid semantic word generation. This phenomenon has indeed been documented (Greenberg, Keane, Ryan, & Verfaellie, 2009; Ryan, Cox, Hayes, & Nadel, 2008; Vallee-Tourangeau, Anthony, & Austin, 1998). Our results suggest that, unlike the episodic condition, during semantic word generation, there was a decrease in gamma power subsequent to the transient increase in gamma power (Figure 2). This decrease possibly reflects an inhibition of the task-irrelevant spatiotemporal information. Indeed, it has been suggested that recovery of task-irrelevant word-related information is not only unproductive but may actually need to be suppressed to allow word generation (Perret, 1974). This claim originally referred to the recovery of semantic information during phonemic word generation. However, the same logic may hold for the recovery of task-irrelevant episodic information during semantic word generation. Thus, an inhibition of task-irrelevant spatiotemporal information is possibly necessary to allow for the recovery of categorical information, essential for semantic word generation. Such recovery is possibly localized in a deep brain region (based on fMRI results) that could not reliably be identified by scalp EEG. Alternatively, it may perhaps occur in a frequency band outside the scope of the current analyses. Only after the additional recovery and verification steps was the word articulated, resulting in a larger time interval between the increase in gamma power in electrode P3 and semantic word articulation. Thus, we suggest that the difference in timing of the gamma increase in the episodic and semantic conditions, relative to word articulation, possibly reflects the dissimilar contribution of spatiotemporal information to the two word generation tasks. This extends the claim that timing and order of activating patterns may differ between encoding and retrieval (Johnson et al., 2015) to different conditions within the retrieval phase.

Remarkably and critically, the three word generation tasks may differ not only in the type of information required for search and post retrieval evaluation but also in their executive function demands (Henry & Crawford, 2004; Perret, 1974). Specifically, it has been suggested that phonemic word generation is more demanding in this respect, as it requires effortful search according to novel rules, while suppressing the habit of using words according to their meaning. This is unlike semantic word generation, which relies on habitual and well-established

search strategies that follow mundane word search strategies for daily use of language. To the best of our knowledge, the relative executive functional demands of the episodic, as compared with the semantic and phonemic, conditions has not been discussed in the literature. This is due to episodic word generation traditionally being tested via free recall tasks. However, when applying the same logic, one may assume that suppression of a words' meaning would be required in the episodic condition as well. Nevertheless, when comparing our results against literature-based predictions, it is unlikely that the gamma pattern seen in electrode P3 corresponds with varying degrees of executive function demands. Although executive control is considered more pertinent to phonemic relative to semantic processing, in this study, the transient increase in gamma power was found for the semantic and episodic conditions, rather than the phonemic condition. In addition, this line of interpretation cannot explain the different timing in the gamma increase between the episodic and semantic conditions. Therefore, although the task may differ in executive function demands, it is unlikely that this difference underpins the EEG pattern seen in the parietal electrode.

One limitation of the present results is the lack of a significant post hoc difference in the phonemic condition (Figure 2C), despite the apparent differences found between the phonemic and other two conditions seen in Figures 1 and 2. This is possibly related to the highly conservative Bonferroni approach taken in post hoc analysis along with the reduced statistical power due to the relatively small sample size. The different timing of gamma increases in the episodic and semantic conditions, along with the inhibition that followed it in the semantic condition, contributed to the larger difference found between the episodic and semantic conditions, with this difference reaching significance in the post hoc analysis.

All three word generation tasks involved both search and evaluation processes, termed retrieval and postretrieval in the memory literature, respectively, and are thought to occur in a serial and repetitive manner (Badre & Wagner, 2007; Raaijmakers & Shiffrin, 1981; Norman & Bobrow, 1979; Collins & Loftus, 1975). Postretrieval operations such as monitoring, selection, evaluation, and verification serve as quality control for recall products that guarantee response aptness in view of current goal and decision criteria. Generation cues affect both retrieval and postretrieval phases (Williams & Hollan, 1979). At retrieval, they provide the starting point for the search phase. At postretrieval, they serve as the decision criteria, determining which details will be examined when evaluating a potential response (Rugg & Allan, 2000). Although retrieval and postretrieval processes were not directly distinguished in this study, the fact that the task-specific transient increases in gamma power were locked to and immediately preceded word articulation imply that they reflect processes related to either the recovery of a potential response or to its postretrieval evaluation, rather than to the search phase that preceded them. This fits previous electrophysiological indications of reactivation of content (Morton et al., 2013) and temporal (Manning et al., 2011) information immediately before episodic word generation. However, task-specific modulations of the effects were not examined in any of these studies. Neural correlates of postretrieval processing common to episodic and semantic memory were identified, including the "right frontal old/new effect" in ERPs (Hayama, Johnson, & Rugg, 2008; Wilding & Rugg, 1996) and the right dorsolateral prefrontal activation in fMRI (Hayama & Rugg, 2009). Although the precuneus previously emerged as being specific to episodic versus semantic tasks (Hayama & Rugg, 2009), EEG signatures of task-specific postretrieval evaluation have not been reported. The results of this study uncover a task-specific signature, whose specificity to postretrieval evaluation should be thoroughly tested in future studies.

In conclusion, increased gamma activity before episodic word generation has been reported (Burke et al., 2014; Sederberg, Schulze-Bonhage, Madsen, Bromfield, Litt, et al., 2007). However, the present results uncover the task specificity of the gamma-band signal that precedes word articulation, revealing its modulation due to task demands. On the basis of the unique demands of episodic task and the correlation between the increased gamma power and precuneus activity, which was restricted to the episodic condition, a spatiotemporal role for this signal is proposed. Future studies are required to determine whether the identified EEG signal can serve as a fingerprint for individual differences in precuneus recruitment during episodic memory (Meir-Hasson, Kinreich, Podlipsky, Hendler, & Intrator, 2014).

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