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Changes in Theta and Beta Oscillations as Signatures of Novel Word Consolidation

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Abstract

■ The complementary learning systems account of word learning states that novel words, like other types of memories, undergo an offline consolidation process during which they are gradually integrated into the neocortical memory network. A fundamental change in the neural representation of a novel word should therefore occur in the hours after learning. The present EEG study tested this hypothesis by investigating whether novel words learned before a 24-hr consolidation period elicited more word-like oscillatory responses than novel words learned immediately before testing. In line with previous studies indicating that theta synchronization reflects lexical access, unfamiliar novel words elicited lower power in the theta

band (4–8 Hz) than existing words. Recently learned words still showed a marginally lower theta increase than existing words, but theta responses to novel words that had been acquired 24 hr earlier were indistinguishable from responses to existing words. Consistent with evidence that beta desynchronization (16–21 Hz) is related to lexical-semantic processing, we found that both unfamiliar and recently learned novel words elicited less beta desynchronization than existing words. In contrast, no difference was found between novel words learned 24 hr earlier and existing words. These data therefore suggest that an offline consolidation period enables novel words to acquire lexically integrated, word-like neural representations. ■

INTRODUCTION

A growing body of evidence suggests that the process of acquiring a novel word is not necessarily complete at the end of a learning task. It has been proposed that “lexicalization,” the integration of a new item into the existing mental lexicon, is a process that largely takes place during the hours and days after initial memory formation (Davis & Gaskell, 2009; Gaskell & Dumay, 2003). The current study was designed to test the hypothesis that offline consolidation during the 24 hr following encoding produces a fundamental change in the neural representation of novel words. Specifically, we investigated whether oscillatory electrophysiological responses to novel words showed more word-like patterns after an offline consolidation period.

According to the complementary learning systems account (McClelland, McNaughton, & O’Reilly, 1995), novel (word) memories are rapidly encoded by the hippocampal system and initially stored in an episodic, nonintegrated fashion. A slower, neocortical learning process is hypothesized to take place following learning, during which novel information is gradually integrated into existing memory networks. This slow interleaving

of old and new information circumvents the problem of catastrophic interference: the loss of existing knowledge because of sudden introduction of novel connections in the network (McClosky & Cohen, 1989). In the context of word learning, integration of the novel memory involves the formation of connections between the novel word and orthographically, phonologically, or semantically related existing words. Thus, the theory predicts that novel words should begin to interact with existing words after an offline consolidation period, during which lexical connections have been established (Davis & Gaskell, 2009; Gaskell & Dumay, 2003).

Empirical support for this hypothesis comes mainly from a series of studies that investigated lexical competition between novel words and their orthographic or phonological neighbors, a process that is thought to require lexical links between competitors. Lexical competition has been shown to emerge only after a consolidation period of several hours to days (e.g., Takashima, Bakker, van Hell, Janzen, & McQueen, 2014; Dumay & Gaskell, 2007, 2012; Tamminen, Payne, Stickgold, Wamsley, & Gaskell, 2010; Tamminen & Gaskell, 2008; Bowers, Davis, & Hanley, 2005; Gaskell & Dumay, 2003). These effects are not limited to the modality in which novel words were acquired, which makes it highly unlikely that they are driven by purely episodic memory (Bakker, Takashima, van Hell, Janzen, & McQueen, 2014; Szmalec, Page, & Duyck, 2012). Furthermore, semantic priming and

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interference effects between novel and existing words have been shown to increase after a consolidation interval (Tamminen & Gaskell, 2013; Clay, Bowers, Davis, & Hanley, 2007), suggesting that semantic integration is similarly affected by offline consolidation.

To shed more light on the neural basis of these behavioral patterns, the current study employed time–frequency analysis of EEG data acquired during retrieval of trained novel words to investigate the development of novel word memories over the course of consolidation. Oscillatory power increase as measured by scalp level EEG reflects the synchronized firing of a population of neurons, a phenomenon that is thought to underlie the formation and activation of cell assemblies representing individual memory traces (Hebb, 1949). Indeed, oscillations have been found to be sensitive to various types of episodic and semantic memory processes (for reviews, see Hanslmayr, Staudigl, & Fellner, 2012; Düzel, Penny, & Burgess, 2010; Nyhus & Curran, 2010; Klimesch, 1999). This sensitivity extends to language processing (for a review, see Bastiaansen & Hagoort, 2006), thus providing a particularly useful window into neural processes at the intersection of language and memory such as those related to word learning. Oscillatory patterns with distinct temporal and spatial features have been shown to be sensitive to various lexical manipulations, including the distinction between real words and pseudowords. Such lexicality effects have been observed in the theta (4–7 Hz), alpha (8–12 Hz), beta (13–30 Hz), and gamma (30–100 Hz) frequency bands.

Power increase in the theta band (4–7 Hz) relative to a prestimulus baseline has been proposed to arise from resonating activity within hippocampal–neocortical loops (Klimesch, 1999; Miller, 1991; Buzsáki, 1989) and is thought to play a crucial role in memory formation. Rhythmic firing of hippocampal cells that are connected to multiple neocortical sites can cause synchronization of these potentially widely distributed cell populations across the cortex. Thus, hippocampus-driven synchronization enables the formation of Hebbian cell assemblies across large distances, binding together multiple representations into a single memory trace. In support of this theory, theta synchronization has been shown to be associated with memory encoding and retrieval. For example, theta power during encoding is usually higher in response to subsequently recalled items and to correctly recognized old items compared to new items during retrieval (for reviews, see Hanslmayr & Staudigl, 2014; Düzel et al., 2010; Nyhus & Curran, 2010; Bastiaansen & Hagoort, 2003).

In line with the involvement of theta synchronization in retrieval of long-term memory traces, theta power increases have also been linked specifically to lexical-semantic access. For example, pseudowords have repeatedly been found to elicit lower theta power than real words (Krause et al., 2006). This difference was largest in the left inferior prefrontal and temporal cortex, known to

be involved in lexical storage (Marinkovic, Rosen, Cox, & Kovacevic, 2012). A larger power increase in left temporal theta was furthermore observed when participants read semantically rich open-class words (nouns, verbs, and adjectives) versus words with less semantic content such as determiners and prepositions (Bastiaansen, van der Linden, Ter Keurs, Dijkstra, & Hagoort, 2005). Interestingly, theta responses have been found to show different topographies for words with meanings related to visual versus auditory properties (Bastiaansen, Oostenveld, Jensen, & Hagoort, 2008). This suggests that theta synchronization reflects not only episodic memory retrieval but also plays a role in the activation of lexical-semantic representations.

Within memory paradigms, the alpha and beta bands have most often been linked to power decreases from baseline, presumably reflecting the desynchronization of local cell assemblies (for a review, see Hanslmayr et al., 2012). During language comprehension, a decrease in alpha power relative to a prestimulus baseline is generally seen at posterior sites (Mellem, Bastiaansen, Pilgrim, Medvedev, & Friedman, 2012; Tavabi, Embick, & Roberts, 2011; Shahin, Picton, & Miller, 2009; Krause et al., 2006; Bastiaansen et al., 2005; Bastiaansen, van Berkum, & Hagoort, 2002; Klimesch et al., 2001) and over left occipitotemporal and central areas in the beta band (Krause et al., 2006; Bastiaansen et al., 2005). Alpha and beta decreases are often interpreted as reflecting visual processing, attention, and memory/task demands (e.g., Shahin et al., 2009; Bastiaansen & Hagoort, 2006; Klimesch et al., 2001). Both bands have however been found to be sensitive to sensory and semantic features of memory traces, suggesting that they may play a specific role in memory retrieval as well as reflecting more general cognitive processes (Hanslmayr et al., 2012).

Gamma oscillations are difficult to observe in scalp level EEG because of their small amplitude and are therefore less often reported in studies investigating lexical processing. Nonetheless, there is strong evidence that they are associated with lexical activation. Larger left hemispheric power in the gamma band in response to words than to pseudowords has been observed in EEG as well as MEG recordings (Krause, Korpilahti, Pörn, Jäntti, & Lang, 1998; Pulvermüller et al., 1996; Lützenberger, Pulvermüller, & Birnbaumer, 1994). Gamma responses furthermore exhibit a distinct topography for nouns versus verbs, which has been claimed to reflect the somatotopic organization of semantic representations (Pulvermüller, Lützenberger, & Preissl, 1999). An intracranial EEG study comparing words, pseudowords, and consonant strings found that gamma effects in the fusiform gyrus and inferior frontal gyrus distinguished mostly between pronounceable and unpronounceable stimuli, indicating an involvement of gamma in prelexical graphemic and phonological processing. However, a power increase specific to semantic processing of words was also observed,

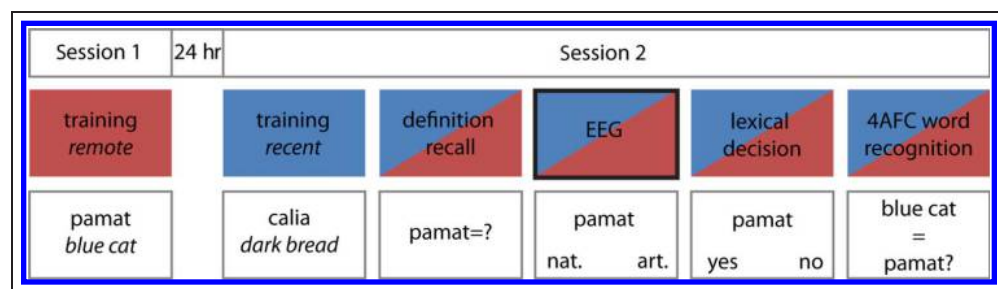
peaking around 400 msec in the pars opercularis (Mainy et al., 2008). Gamma synchronization thus appears to be involved in the activation of local lexical-semantic networks.

In summary, previous findings suggest that a left-lateralized frontotemporal power increase from baseline in the theta and gamma bands, a posterior decrease in the alpha band, and a central or left-lateralized decrease in the beta band constitute the oscillatory signatures of lexical-semantic processing. In the current study, we exploited this pattern to test the hypothesis that offline consolidation facilitates integration of novel words into the neocortical lexical network, leading to a gradually more word-like response over the course of consolidation. To this end, we compared novel words to existing words at three stages of lexicalization: untrained words, words learned immediately before testing, and words learned 24 hr previously.

Comparing the two extreme sides of the scale, untrained novel words versus untrained existing words, we can expect to see the clearest difference in oscillatory patterns. Specifically, we predicted that untrained novel words would elicit a smaller increase in theta and gamma power and a smaller decrease in alpha and beta power than untrained existing words. At the next stage, immediately after learning, novel words may start to exhibit some word-like characteristics in their oscillatory response. If consolidation, however, indeed changes the nature of a novel word's memory representation, we should observe an even larger decrease in the difference between novel words and existing words when they are retrieved after a 24-hr interval. If lexicalization is complete, then the differences predicted between untrained novel words and existing words may be entirely absent after this 1-day interval.

Novel words learned before the 24-hr consolidation period would also be expected to show behavioral effects of lexicalization, unlike novel words trained immediately before test. We therefore investigated whether trained novel words were able to influence recognition of their existing orthographic neighbors in a lexical decision task. Competition between novel and existing words, as indicated by slower RTs to existing words with newly learned neighbors, would suggest integration of the novel words into the existing mental lexicon.

Figure 1. Schematic overview of the tasks. The bottom row gives an abbreviated example of a trial. Participants learned two sets of novel words with an interval of 24 hr and were tested on both sets (recent and remote) immediately following the second training session.



METHODS

Participants

Twenty-two native Dutch-speaking participants (six men), aged 18–28 years (mean = 21 years), gave written informed consent to participate in the experiment. Participants reported no history of neurological or language-related disorders and had normal or corrected-to-normal vision and hearing. All participants were right-handed as assessed by an abridged version of the Edinburgh Handedness Inventory (Oldfield, 1971). They received course credit or were paid for their participation.

Materials

Four lists of 20 novel words of 5–7 letters (mean = 5.9) were created by substituting one letter of an existing Dutch word, for example “pamat” from “patat” (chips). The substituted letter was in the first position in nine words, between second and penultimate position in 59 words, and in last position in 12 words. Lists were matched on word length and on the frequency of occurrence of the existing neighbor (0–175 per million, mean = 23.8) according to the CELEX database (Baayen, Piepenbrock, & Gulikers, 1995).

Two lists of 20 definitions were created to provide the novel words' meanings, in part based on Tamminen and Gaskell (2013). Each definition consisted of an object category paired with two distinguishing features, for example, “A cat that has stripes and is bluish gray.” For each participant, two lists of novel words and both lists of definitions served as the to-be-learned material, one in each of two learning sessions. The pairing of words and definitions was randomized for each participant.

Sixty existing Dutch words were divided in three lists of 20 words, matched on frequency (1–195, mean = 33.6) and length (5–7 letters, mean = 6). Each existing word was presented with a realistic definition (e.g., “lemon: a yellow, sour-tasting fruit”). Participants saw two of the three lists of existing words and definitions, one in each of the two learning sessions.

Design and Procedure

The experiment consisted of two training sessions followed by a test phase (Figure 1). In both sessions, participants

learned a set of novel and existing words paired with a definition. Approximately 1 hr after completion of the second training session, EEG responses were recorded while participants read the trained novel and existing words from both sessions, as well as untrained novel and existing words. This design thus allowed us to compare novel and existing words at each of the three stages of lexicalization: untrained, learned but unconsolidated, and consolidated. The inclusion of existing words in both training sessions created a situation in which novel and existing words at each lexicalization stage were equated as much as possible with respect to recent exposure and episodic memory status. The trained existing words therefore provided an unbiased “baseline” against which the lexical status of the novel words could be assessed. In a second EEG task, participants saw existing Dutch words primed by either semantically related or unrelated learned novel words. Data from this task are reported elsewhere (Bakker, Takashima, van Hell, Janzen, & McQueen, submitted). After the EEG session, participants performed a lexical decision task on the existing orthographic neighbors of the learned novel words, which served to measure the behavioral consequences of consolidation.

Training and Memory Tests

The training phase started with an initial round of 5-sec visual presentations of each of the 20 novel and 20 existing words with their definitions. Four training tasks followed, in fixed order: (1) two-alternative-forced-choice (2AFC) word–definition matching where definitions were the cues and words were the choices, three trials for each item; (2) 2AFC word–definition matching where words were the cues and definitions were the choices, three trials for each item; (3) recall of words cued by definitions; and (4) recall of definitions cued by words. There was no RT limit. Participants gave their responses by pressing a key or typing on the keyboard, after which the correct response remained on the screen for 3 sec. Item order was randomized within each task. This series of training tasks was repeated once more, giving 17 exposures per word in total. The training procedure was identical in Sessions 1 and 2. The assignment of word lists to conditions (untrained, recent, and remote) was counterbalanced across participants.

Immediately after the training phase in the second session an additional block of definition recall was presented without feedback, containing all words from both sessions. This block served both to assess memory and as a reactivation of the remote condition to reduce any differences in perceptual processing between conditions because of recency of exposure. At the end of the session, after the EEG recording, a block of 4AFC word–definition matching was administered. This task served to confirm that recognition memory was good enough to assume that learning had been successful and no excessive forgetting of the remote condition had occurred.

EEG Task

After a short break and preparation of the EEG setup, which took approximately 1 hr in total, the EEG session was started. Participants were presented with the novel and existing words learned in Session 1 (remote condition), novel and existing words learned in Session 2 (recent condition), and a set of 20 novel and 20 existing words not presented during training (untrained condition). Each item was presented five times, with at least 40 trials separating instances of the same item. To encourage semantic processing, participants were prompted to make a semantic decision after 70% of trials. In half of these trials, they were asked to indicate whether the presented word was an artifact or a natural object, and in the other half they decided whether the object was bigger or smaller than a shoebox. Responses were given by pressing one of two buttons, counterbalanced across participants. The unpredictability of the presence and nature of the question was introduced to discourage participants from preparing a motor response before the question prompt, thus minimizing response- and muscle-related contamination of the EEG signal. Untrained novel words, which had no meaning, were never followed by a question. Trials started with a 600-msec baseline during which a fixation cross was presented, followed by the target word presentation for 1000 msec. On question trials, the prompt then appeared and stayed on the screen for 1000 msec. Participants had to respond during the window in which the prompt was present. Each trial was followed by a 1000-msec period in which participants were free to blink.

Lexical Decision Task

In this task, participants responded to the existing orthographic neighbors of the trained novel words (e.g., “patat” when “pamat” had been learned), as well as neighbors of the untrained list of novel words. If novel words are lexically integrated, competition for selection should slow down recognition of their neighbors relative to control words without novel competitors. Words were presented on the screen for 2000 msec or until the participant responded, with a 750-msec interval separating trials. Participants were instructed to respond as fast as possible by pressing one of two buttons. Real words included the existing neighbors of the learned novel words from the remote and recent conditions and the neighbors of the two untrained lists of novel words, giving 80 word trials in total. A set of 80 unrelated pseudowords, matched in length with the real words, was created to serve as “no”-response trials. Trial order was randomized for each participant.

EEG Acquisition and Preprocessing

Continuous EEG was recorded from 59 electrodes spaced equidistantly on an Acticap systems cap (Brain Products

GmbH, Gilching, Germany), amplified with a BrainAmps (Brain Products) DC amplifier (500 Hz sampling rate, 0.1–1000 Hz cutoff), referenced online to the left mastoid. EOG was recorded from two electrodes placed at the temples and two placed above and below the left eye. Impedances were kept below 20 k Ω .

EEG preprocessing and analysis was done using the Fieldtrip toolbox (Oostenveld, Maris, Fries, & Schoffelen, 2011). The signal was re-referenced offline to the averaged left and right mastoids, and a band-stop filter at 50, 100, and 150 Hz was applied to remove line noise. Epochs of 400 msec prestimulus to 1000 msec poststimulus were extracted. Trials containing muscle or hardware noise were rejected (6.3%), and noisy channels were interpolated using the averaged signal of neighboring channels. Eye blinks were removed using independent component analysis. At least 70 trials per condition (average 92) remained for each participant.

EEG Analysis

For frequencies in the 4–30 Hz range, time–frequency representations (TFRs) were computed using a 400-msec sliding Hanning window followed by a Fourier transform. Data were analyzed between 200 msec prestimulus and 700 msec poststimulus, in steps of 50 msec and 1 Hz. For frequencies in the 30–100 Hz range, we used a multitaper approach with 200 msec discrete prolate spheroidal sequence windows, in steps of 50 msec and 1 Hz with 8 Hz frequency smoothing.

The average signal change relative to a 200–100 msec prestimulus baseline was computed across all six conditions: novel untrained, novel recent, novel remote, existing untrained, existing recent, and existing remote. On the basis of visual inspection of the average TFR across all conditions, we selected time–frequency windows that showed maximal effects (Figure 3A). To define spatial ROI(s), channel selections for each time–frequency window were made based on the topography of the averaged responses (Figure 3B). On the basis of evidence that there may be various subbands within the classical alpha and beta frequency bands, which show distinct response patterns and reflect different cognitive processes (Weiss & Mueller, 2012; Klimesch, 1999), we did not average across these entire frequency ranges but rather selected narrower bands based on the average TFR. This method—selecting all ROIs based on the average response across conditions—ensured that time/frequency/channel ROI selection was unbiased by the condition differences under investigation.

To quantify the effect of consolidation on the lexical nature of novel word processing, we computed a normalized difference between raw power values in the novel and existing conditions ($[\text{novel} - \text{existing}] / [\text{novel} + \text{existing}]$) on each level of training. Within each spatial ROI, training effects were tested with a one-way repeated-measures ANOVA with levels untrained, recent, and remote.

Lexicality effects at each level of training were tested with one-sample t tests.

In many previous studies, the subject-average ERP was subtracted from each trial before computing the TFR to isolate induced activity. However, this approach may not be optimal given that the ERP varies across trials within a single subject. Following Bastiaansen et al. (2008), we therefore computed the TFR of the ERP between 4 and 30 Hz and applied the same statistical analysis as done on the TFRs to investigate if any time–frequency effects were driven by evoked activity. For ERP analysis, data were band-pass filtered at 1–30 Hz and baseline-corrected to a 200–100 msec prestimulus baseline before computing the TFR.

RESULTS

Behavioral Results

Memory Performance

In the definition recall test following the training phase in Session 2, participants remembered significantly more features from the definitions of the recent (88.5%) than of the remote words (51.4%; $t(21) = 11.67, p < .001$; see Figure 2A). Recognition of words cued by their definitions in the 4AFC task at the end of Session 2 was near ceiling for the remote as well as the recent condition (98.2% for both; see Figure 2B). Together, these results suggest that, although some forgetting had taken place, memory representations of most words were still retrievable after 24 hr.

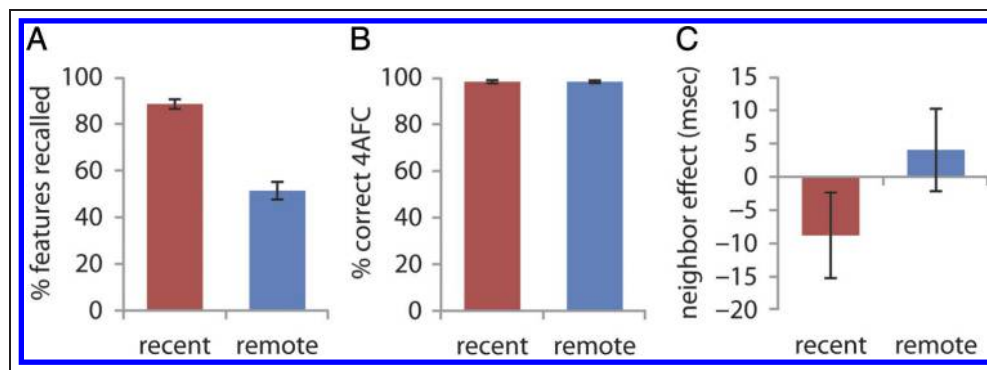
Lexical Competition

Accuracy in the lexical decision task was high (97.1%) and did not differ between neighbors of recent and remote novel words ($p > .05$). For the RT analysis, misses and RTs more than 1.5 standard deviation from the mean were removed (9.9%). We found a trend toward facilitation in the recent condition: Neighbors of recent novel words were recognized 12 msec faster than control words, $t(21) = 1.99, p = .059$. This effect changed significantly after 24 hr, $t(21) = 2.14, p = .044$, turning into minimal, nonsignificant inhibition in the remote condition, $t(21) = 0.21, p = .836$. Thus, although no behavioral evidence of lexical competition was found after the 1-day delay, these results do suggest that a change in the novel words' behavior occurred following offline consolidation (see Figure 2C).

Semantic Decision during EEG

The semantic decision task to novel words was difficult, as indicated by low accuracy (recent 53.7%, remote 54.6%), which, however, was above chance (recent: $t(19) = 2.57, p = .019$; remote: $t(19) = 2.71, p = .014$). There was no difference between the two conditions ($p > .05$).

Figure 2. Behavioral results. (A) Percentage of definition features correctly recalled in Session 2. Performance was significantly better in the recent condition. (B) Percentage of correctly chosen words when cued by a definition in the 4AFC task in Session 2. (C) Difference in lexical decision latencies between base words of trained novel words and control words. A marginal facilitation effect (faster responses to words with novel neighbors) was observed in the recent condition, which was significantly reduced in the remote condition. Error bars in all panels denote standard errors.



Good performance on the existing words confirmed that participants did attend to the task (recent 90.6%, remote 89.7%, untrained 90.9%).

EEG Results

The averaged TFR across all conditions (see Figure 3A, C) showed an early theta (4–7 Hz) power increase at 100–300 msec, peaking over occipital electrodes (denoted as $\theta 1$ in Figure 3). This effect was followed by a longer-

lasting increase between 400 and 700 msec with a distinct frontotemporal distribution ($\theta 2$ in Figure 3). A power reduction was observed between 300 and 500 msec in the upper alpha band (10–12 Hz), with an occipital peak and a weaker frontal component. There was no broadband beta modulation, but rather two frequency components with distinct latencies and topographical distributions. At lower beta frequencies ($\beta 1$ in Figure 3, 16–21 Hz), power decreased over a posterior as well as a left-central region between 300 and 500 msec. Power

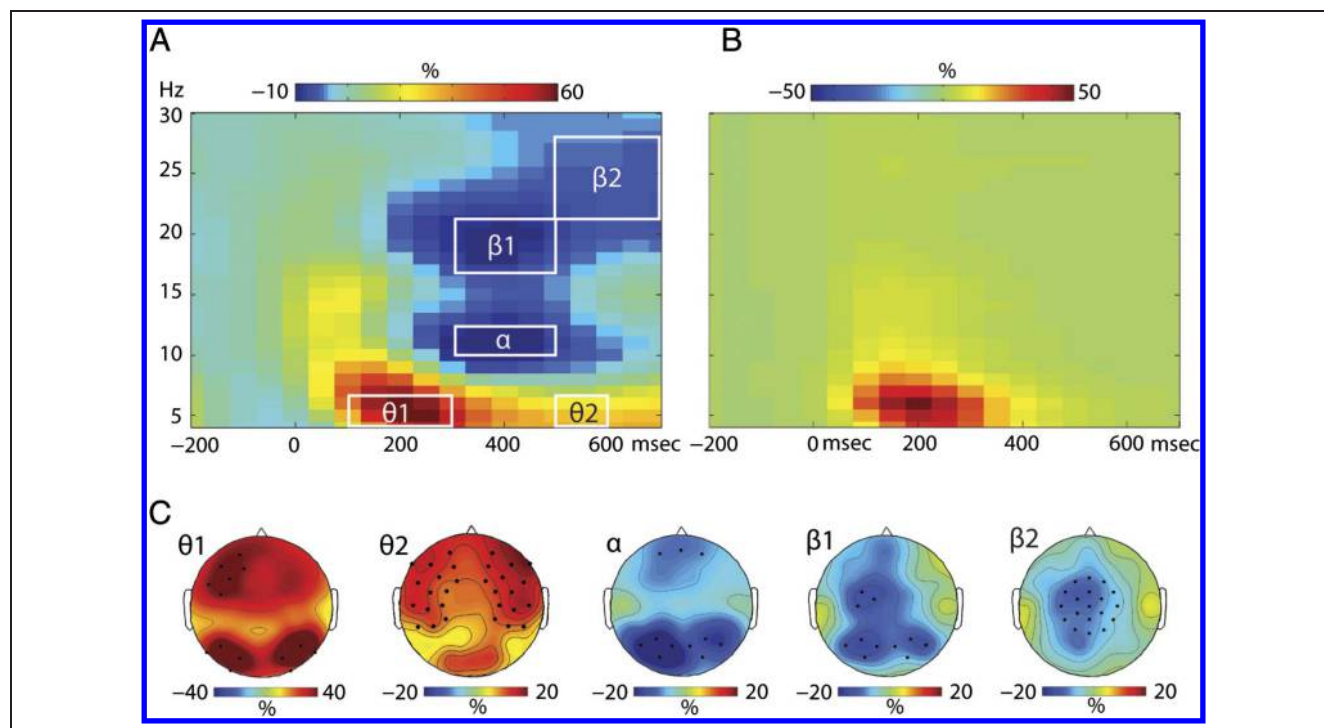
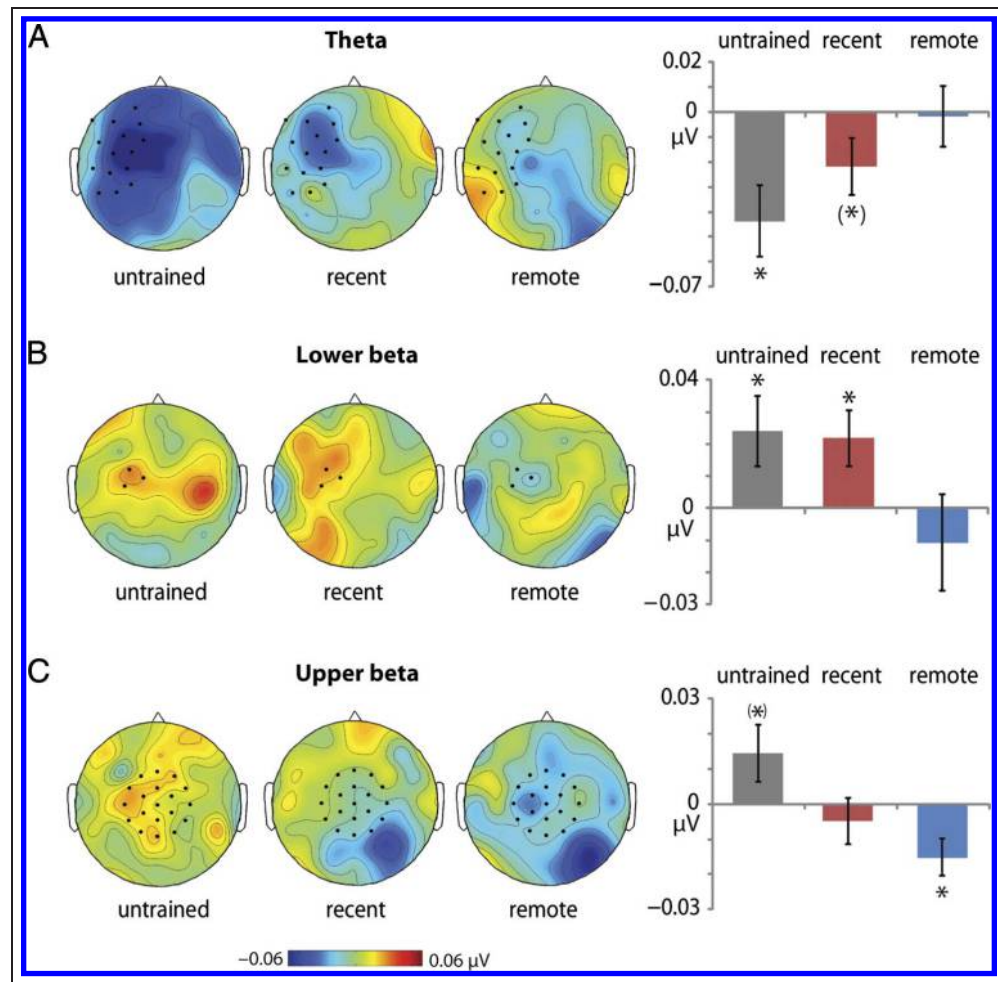


Figure 3. (A) TFR showing the percent power change relative to a baseline period of –200 to –100 msec prestimulus, averaged across all conditions and all sensors. Rectangles indicate the time–frequency windows of interest in which condition differences were analyzed. (B) TFR of the ERP, representing evoked activity in the power spectrum. (C) Topography of the selected time–frequency windows highlighted in the average TFR, plotting percentage change from baseline. Black dots indicate channels selected for analysis of condition effects.

Figure 4. Topoplots and ROI averages of the normalized difference between novel and existing words at each training level. Blue colors indicate lower power for novel words than existing words; red colors indicate higher power for novel than existing words. Black dots indicate the ROIs selected based on the maximum effect in the average TFR (Figure 3A). Bars represent the average across the highlighted channels; error bars denote standard errors. (A) Novel-existing difference in the theta band (4–8 Hz). Novel words elicited less theta power than existing words in the untrained condition and marginally less in the recent condition, whereas responses to novel and existing words were identical in the remote condition. (B) Novel-existing difference in the lower beta band (16–21 Hz). Both untrained and recent words elicited higher beta power (less desynchronization) than existing words, but there was no difference in the remote condition. (C) Novel-existing differences in the higher beta band (21–28 Hz). Novel words elicited marginally higher power (less desynchronization) in the untrained condition and significantly less power (more desynchronization) in the remote condition.



in a higher beta frequency band (β_2 in Figure 3, 21–28 Hz), on the other hand, decreased over vertex electrodes in a later window of 500–700 msec. No effects were found in the gamma band, which will therefore not be reported on further.

Theta (4–7 Hz)

No effects of condition were found in the early theta window (θ_1 , 100–300 msec), either over occipital or frontal channels ($p > .05$). The second theta power increase over bilateral frontotemporal channels emerged around 400 msec and lasted until the end of the analysis window (θ_2 ; see Figure 3A, C). Condition effects were tested in the center of this window (500–600 msec). No effect of condition was seen in the right hemisphere ROI ($p > .05$). In contrast, lexicity differences in the left hemisphere decreased over time, $F(2, 42) = 3.433$, $p = .049$ (Figure 4A). Untrained novel words elicited significantly less theta synchronization than existing words, $t(21) =$

2.94 , $p = .008$. In the recent condition, only a trend toward a lexicity effect in the same direction remained, $t(21) = 1.88$, $p = .075$, whereas remote novel words were no longer distinguishable from existing words, $t(21) = 0.24$, $p = .811$. The size of the lexicity effect significantly decreased between the untrained and remote conditions, $t(21) = 2.519$, $p = .02$, but not between the untrained and recent or between the recent and remote conditions (both $p > .05$), suggesting that both exposure and consolidation played a crucial part in the emergence of the word-like theta response to the novel words.

Alpha (10–12 Hz)

The average TFR across all conditions showed a desynchronization in the upper alpha band, peaking between 300 and 500 msec over left posterior and frontal channels (see Figure 3). No effect of training was found on the magnitude of this effect ($p > .05$), indicating that the alpha decrease reflected nonlexical processes.

Lower Beta (16–21 Hz)

A desynchronization between 16 and 21 Hz was visible in the average TFR, peaking around 300–500 msec (Figure 3). An ANOVA on the averages within the left-central ROI revealed an effect of Training, $F(2, 42) = 4.18, p = .022$. Follow-up tests showed that whereas both untrained and recently learned novel words elicited weaker desynchronization than existing words (untrained vs. existing: $t(21) = 2.2, p = .039$; recently learned vs. existing: $t(21) = 2.53, p = .019$), there was no difference between novel and existing words in the remote condition ($p = .49$), suggesting a specific sensitivity to consolidation in this frequency band. This pattern is illustrated in Figure 4B. No effects were found in the left and right occipital ROIs ($p > .05$), which may be related to the same lower-level processes underlying the upper alpha decrease.

Upper Beta (21–28 Hz)

A later and more centrally distributed desynchronization emerged in a higher beta frequency band, around 500–700 msec. This effect also changed across training levels, $F(2, 42) = 6.39, p = .003$, but unlike in the lower beta band, the pattern appeared to be less influenced by consolidation alone (see Figure 4C). As expected, untrained novel words elicited numerically weaker desynchronization than existing words, although this effect did not reach significance, $t(21) = 1.78, p = .089$. The recent condition did not show any sign of a lexicality effect, $t(21) = 0.83, p = .415$, suggesting that training alone sufficed to evoke a word-like response. Interestingly, a reverse lexicality effect was found in the remote condition, where desynchronization was *stronger* for novel than existing words, $t(21) = 2.6, p = .017$.

ERP Analysis

ERP analysis (Figure 3B) indicated that the early theta increase (θ_1) was driven by evoked activity, reflecting the visual P1–N1 complex, which has a cycle of approximately 150 msec or 6 Hz. The lack of power modulations of the ERP in any other windows suggests that the effects reported above reflected mainly induced activity. To test this, we repeated all power analyses on the TFR of the ERP, which confirmed that there was no effect of condition in any of the selected time–frequency windows (all $ps > .05$).

Combined EEG and Behavioral Results

To investigate the relation between behavior and oscillatory activity more directly, we correlated the lexical competition effect with the theta and beta lexicality effects in the remote condition. In the theta band, no correlation was observed, $r(20) = -.001, p = .999$. The lower beta band exhibited a numerical effect in the expected direc-

tion (the larger the competition effect, the smaller the difference between remote novel and existing words), which however did not reach significance, $r(20) = -.22, p = .186$.

DISCUSSION

This study investigated the electrophysiological effect of novel word consolidation as reflected in changes in brain oscillations, under the hypothesis that words learned prior to an offline consolidation opportunity elicit more word-like power modulations. In agreement with previous studies, word presentation caused a power increase in the theta band around 500 msec as well as reductions in alpha and beta power between 300 and 700 msec. We did not however find the previously reported synchronization in the gamma range, possibly because of the low sensitivity of scalp-recorded EEG to the small amplitude that characterizes high frequency oscillations. Clear consolidation effects were observed in the theta band over left-temporal channels and in the lower beta band in a left-central region. These data suggest that offline consolidation contributes to lexicalization of novel words, a process that appears to affect theta and lower beta frequencies especially.

Untrained novel words (i.e., pseudowords) elicited lower theta power than existing words over left fronto-temporal channels, in line with previous findings of lexicality effects localized to the left frontal and temporal cortex (Marinkovic et al., 2012; Krause et al., 2006). This difference weakened when novel words had been learned immediately before testing, but novel words became indistinguishable from real words only after a 24-hr consolidation period. It has been argued that somatotopically organized cell assemblies underlie lexical-semantic representations (Pulvermüller, 1999), which require synchronized firing to “ignite” and enable word recognition. In support of the idea that theta synchronization may provide such a mechanism, Bastiaansen et al. (2008) showed a meaning-dependent spatial distribution of theta power: names of colors and shapes elicited stronger synchronization at occipital electrodes, whereas words referring to sounds increased theta power over the auditory cortex. Although Pulvermüller’s (1999) proposal linked gamma frequencies to the reverberation of such lexical cell assemblies, Bastiaansen et al.’s data suggest that theta synchronization may also play a crucial role in their activation (see also Miller, 1999). The current data thus indicate that retrieval of consolidated words, but not unconsolidated words, involved the type of lexical retrieval process that is supported by theta synchronization, rather than an episodic retrieval process.

A step-like effect of consolidation was observed over left-central channels in the lower beta band (16–21 Hz). At 500–700 msec after word onset, untrained and recent words showed identical lexicality effects, whereas remote

novel words did not differ from existing words. The lexicality effect for untrained words is consistent with previous reports of stronger beta power decreases for words versus pseudowords (Krause et al., 2006; Klimesch et al., 2001). Beta effects during language processing are often attributed to attentional differences between conditions (e.g., Shahin et al., 2009; Bastiaansen et al., 2005). However, in the current paradigm, it is not clear why consolidated words should have demanded more attention than unconsolidated or untrained words.

A more plausible explanation of the present findings therefore is that desynchronization in the lower beta band indexes the semantic richness of the memory being retrieved (Hanslmayr et al., 2012). This claim is supported by several findings indicating a relation between beta desynchronization and deep semantic processing during encoding, which are highly similar to the current results in latency, frequency, and topography. For example, beta decreases during word encoding were found to be stronger in a semantic animacy judgment task compared to a shallow alphabetic task and predicted later recall only in the semantic task (Hanslmayr, Spitzer, & Bäuml, 2009). Hanslmayr et al. (2011) as well as Meeuwissen, Takashima, Fernández, and Jensen (2011) localized subsequent memory effects in the lower beta band to the left inferior frontal gyrus, which is known to be involved in semantic processing. Accordingly, stronger beta desynchronization in relation to semantic richness has also been found in sentence processing tasks without an episodic encoding component (Mellem et al., 2012; Shahin et al., 2009; Bastiaansen et al., 2005).

Together, these results support the idea that the beta desynchronization effect in the current data reflects retrieval of semantic memory traces. Interestingly, unconsolidated novel words behaved like pseudowords rather than consolidated or existing words, although the task encouraged similar levels of semantic processing for both recent and remote items. Given the evidence for involvement of beta desynchronization in semantic access, this pattern therefore suggests that consolidation increased the semantic content of remote novel word memories. This may be a result of consolidation of links between the novel lexical representation and its (possibly nonlinguistic) semantic features but may additionally involve the formation of direct interlexical connections with semantically related words. Behavioral semantic priming paradigms may be able to shed light on the precise relation between beta desynchronization and semantic integration.

In contrast, a centrally distributed power decrease in the upper beta band (21–28 Hz) showed a more complex pattern. Untrained words elicited marginally weaker beta desynchronization than existing words, similar to the lower beta effect, but recent words did not. Most surprisingly, remote words induced *stronger* beta desynchronization than existing words. The late time window, extending past the end of the analyzed epoch, and the central distribution

of this effect point to a response-related explanation. Beta desynchronization over central channels has often been linked to motor preparation and imagery, both of limbs (De Lange, Jensen, Bauer, & Toni, 2008) and of speech (Piai, Roelofs, & Maris, 2014; Fisher et al., 2008), and has been shown to increase with response certainty (Alegre et al., 2004). Given that untrained novel words did not activate a representation based on which a response could be prepared, but existing words did, the larger desynchronization response to untrained existing versus novel words may reflect selective motor preparation for the existing words. More difficult to explain is the stronger desynchronization to remote novel words compared to existing words. This difference could be related to attention or response uncertainty, but in any case appears to reflect task-related effects rather than changes because of lexicalization.

Unlike several studies that have reported lexicality effects around 8–12 Hz (Tavabi et al., 2011; Krause et al., 2006; Bastiaansen et al., 2005; Klimesch et al., 2001), we did not observe any effects of lexicality or consolidation in the alpha band. The occipital distribution indicates that this power decrease reflects visual processing and attention, as has been argued before (e.g., Bastiaansen et al., 2005; Klimesch et al., 2001). In a regular lexical decision task, real words are likely to attract more attentional resources than meaningless pseudowords. In the current study, in contrast, the sharp distinction between words and pseudowords was blurred by the introduction of meaningful, partly lexicalized novel words. This may have led to more attentive and elaborate processing of all stimuli, perhaps including a more tolerant lexical search, which reduced the difference between words and pseudowords.

Although the theta and lower beta frequency bands showed clear effects of novel word consolidation, we did not find straightforward behavioral evidence of lexical competition in the lexical decision task. One reason for this could be that, although novel word memories underwent a representational change, as indicated by the oscillatory data, this process did not involve integration to the degree necessary for lexical competition. Instead, consolidation may have simply led to a strengthening of the novel memory traces and their semantic associations, without development of direct lexical connections. This would be part of the process termed “lexical configuration” by Leach and Samuel (2007): The formation of a long-lasting representation encoding all the available factual information associated with a word, as distinct from the integration of that information into the existing lexicon (“lexical engagement” according to Leach and Samuel).

An alternative explanation is that some degree of integration did take place during the consolidation period but was not picked up behaviorally by the lexical decision task. Assuming this is the case, a possible explanation for the lack of a competition effect between remote novel words and their existing neighbors lies in the fact that

stimuli were presented visually, rather than auditorily, as in previous studies using lexical decision (Tamminen, Lambon Ralph, & Lewis, 2013; Szmalec et al., 2012; Tamminen & Gaskell, 2008; Gaskell & Dumay, 2003). Whereas a higher number of neighbors consistently delays RTs in spoken word recognition paradigms with existing words, effects of existing word neighborhood density in visual lexical decision paradigms have been more mixed (Ziegler, Muneaux, & Grainger, 2003). Several studies have reported null effects or even faster recognition of words with high neighborhood densities in lexical decision (for a review, see Andrews, 1997). These effects have been interpreted as facilitation of a “yes” response when multiple activated neighbors increase the overall orthographic activation in the system (Yates, Locker, & Simpson, 2004). This may explain why the addition of a novel competitor did not increase RTs to existing neighbors in the remote condition, unlike in tasks where meaning access is required, such as semantic categorization. Competition effects have been found in this type of task even when stimuli are presented visually (Bakker et al., 2014; Bowers et al., 2005). The latter type of paradigm therefore seems better suited to investigate lexical integration with visual stimuli.

The trend toward facilitation that was apparent in the recent condition has been observed in auditory lexical decision as well (Tamminen et al., 2010; Gaskell & Dumay, 2003) and presumably reflects episodic priming of the target words by exposure to their novel neighbors. The significant decrease in facilitation after 24 hr may therefore reflect decay of this episodic memory trace, the emergence of integrated lexicalized representations, or a combination of both. Considering the previous evidence for lexical integration from other paradigms (Bakker et al., 2014; Dumay & Gaskell, 2007, 2012; Tamminen et al., 2010; Tamminen & Gaskell, 2008; Bowers et al., 2005; Gaskell & Dumay, 2003) and the fact that oscillatory responses to novel words became more word-like after consolidation, it seems unlikely that no lexicalization had taken place. Thus, although the absence of competition prohibits strong conclusions about the lexical status of the novel words, the observed pattern is compatible with previous findings suggesting a consolidation-dependent development from episodic to lexicalized representations. A more sensitive behavioral task would be instrumental in distinguishing between the contributions of lexical configuration and lexical engagement or integration to the development of the oscillatory response.

This study provides the first electrophysiological support in the frequency domain for the idea that novel word representations undergo a fundamental change in the hours after learning. This change was observable in theta and lower beta oscillatory activity. Given the evidence that theta indexes activation of lexical representations (Bastiaansen et al., 2005, 2008), the fact that theta responses to novel words gradually became more word-like after consolidation confirms that offline consolidation

facilitates lexicalization. A more step-like effect of consolidation (compare Figure 4A and B) was observed in the lower beta band, which is thought to play a role in semantic processing (e.g., Hanslmayr et al., 2012). Thus, the more word-like beta response to consolidated novel words is consistent with the notion of neocortical integration with semantically related existing words during offline consolidation. In conclusion, our data support the hypothesis that offline consolidation facilitates the formation of lexical representations and demonstrate the suitability of time–frequency analysis as a method to explore the neural mechanisms underlying novel word learning.

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