

Theta-band Oscillations in the Middle Temporal Gyrus Reflect Novel Word Consolidation

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Abstract

■ Like many other types of memory formation, novel word learning benefits from an offline consolidation period after the initial encoding phase. A previous EEG study has shown that retrieval of novel words elicited more word-like-induced electrophysiological brain activity in the theta band after consolidation [Bakker, I., Takashima, A., van Hell, J. G., Janzen, G., & McQueen, J. M. Changes in theta and beta oscillations as signatures of novel word consolidation. *Journal of Cognitive Neuroscience*, 27, 1286–1297, 2015]. This suggests that theta-band oscillations play a role in lexicalization, but it has not been demonstrated that this effect is directly caused by the formation of lexical representations. This study used magnetoencephalography to localize the theta consolidation effect to the left posterior middle temporal gyrus (pMTG), a region known to be involved in lexical storage.

Both untrained novel words and words learned immediately before test elicited lower theta power during retrieval than existing words in this region. After a 24-hr consolidation period, the difference between novel and existing words decreased significantly, most strongly in the left pMTG. The magnitude of the decrease after consolidation correlated with an increase in behavioral competition effects between novel words and existing words with similar spelling, reflecting functional integration into the mental lexicon. These results thus provide new evidence that consolidation aids the development of lexical representations mediated by the left pMTG. Theta synchronization may enable lexical access by facilitating the simultaneous activation of distributed semantic, phonological, and orthographic representations that are bound together in the pMTG. ■

INTRODUCTION

Novel word learning, like other types of memory encoding, benefits from an offline consolidation period after exposure. For instance, behavioral work has shown that only after a delay of at least several hours do novel words acquire the ability to enter into lexical competition with phonologically and orthographically similar existing words during speech processing (Bakker, Takashima, van Hell, Janzen, & McQueen, 2014; Gaskell & Dumay, 2003; Dumay & Gaskell, 2007, 2012) and visual processing (Bakker et al., 2014). Similarly, novel words start priming visually presented, semantically related existing words after a delay (van der Ven, Takashima, Segers, & Verhoeven, 2015; Tamminen & Gaskell, 2013).

In line with neurocognitive complementary learning systems (CLS) models of memory consolidation (Frankland & Bontempi, 2005; McClelland, McNaughton, & O'Reilly, 1995; Squire & Alvarez, 1995; Marr, 1970), it has been argued that novel words are initially encoded as episodic memories by a fast-learning hippocampal mechanism and only gradually become integrated into the neocortical lexicon (Davis & Gaskell, 2009). This offline consolidation

process transforms isolated, episodic memories into stable, lexical representations that interact with other words during language use. These representations are no longer modality specific, as indicated by the finding that visually acquired novel words interact with existing words in auditory tasks, and vice versa (Bakker et al., 2014). The CLS account of word learning thus predicts a qualitative change in the neural representation of novel words, with consolidation leading to increasingly word-like retrieval processes.

In previous work (Bakker, Takashima, van Hell, Janzen, & McQueen, 2015), we tested this hypothesis in the time–frequency domain using EEG and demonstrated that consolidated novel words indeed elicited more word-like oscillatory brain responses than recently learned words in the theta band (4–8 Hz) over left-hemisphere sensors. Given that scalp-recorded EEG is not optimized for accurate estimation of distributed neural sources, the question that arises is what the neural substrate of this theta effect is. If consolidation facilitates the formation of lexical representations, enhanced retrieval activity for consolidated novel words should be observed in a relatively focal network of left-lateralized perisylvian regions known to be involved in lexical processing, as will be discussed below. However, the data leave open the possibility that theta synchronization reflects orthogonal processes, for example, those related to episodic retrieval. The current

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study sought to address this issue by using magnetoencephalography (MEG) source localization techniques to identify the sources of the oscillatory signatures of lexical consolidation.

In our previous EEG study (Bakker et al., 2015), the pattern of theta power modulations induced by the visual presentation of a word was taken as a measure of lexical activation. A larger theta power increase versus a pre-stimulus baseline is typically observed in response to words compared with pseudowords, both auditorily (Krause et al., 2006) and visually (Marinkovic, Rosen, Cox, & Kovacevic, 2012). Semantically rich words also elicit larger theta power increases compared with function words (Bastiaansen, van der Linden, ter Keurs, Dijkstra, & Hagoort, 2005). The topography of this power increase is further sensitive to word meaning, possibly reflecting the somatotopic organization of semantic information (Bastiaansen, Oostenveld, Jensen, & Hagoort, 2008). These findings suggest that theta synchronization plays a role in lexical retrieval, which in turn implies that consolidated novel words should exhibit more word-like theta responses than recently learned words.

To test this prediction, participants in the Bakker et al. (2015) study were trained on two sets of novel and existing words paired with definitions, one set on each of 2 consecutive days. After the second training session, EEG responses were recorded as participants made semantic decisions to words from the two trained sets or a set of untrained novel and existing words. It was therefore possible to contrast responses to completely novel words (the “untrained” condition), novel words learned only before test (the “recent” condition), and novel words that had an opportunity for offline consolidation as they had been learned 1 day before testing (the “remote” condition) against existing words with the same level of training and exposure. In line with previous findings, a lexicality effect was observed, as reflected by a larger theta power increase over left-hemisphere temporal sensors in response to untrained existing words than to untrained novel words (i.e., pseudowords). This lexicality effect was smaller in the recent condition but was no longer present for words trained a day earlier (the remote condition). This suggests that the retrieval process became more word-like with consolidation. We speculated that this pattern may reflect the gradual formation of a lexical representation.

The question that arises is where the neural substrate of the theta-related lexicalization process might be located. A likely candidate is the left posterior middle temporal gyrus (pMTG), which many current models of word processing view as a lexical “hub” that mediates the mapping of word forms onto distributed semantic information (Gow, 2012; Lau, Phillips, & Poeppel, 2008; Hickok & Poeppel, 2004, 2007). The role of the left pMTG in lexical processing is supported by fMRI evidence showing an enhanced BOLD response to words relative to pseudowords (Prabhakaran, Blumstein, Myers, Hutchison, & Britton,

2006) as well as by semantic priming effects in both fMRI and EEG (see Lau et al., 2008, for a review). Damage to the left pMTG typically results in word finding problems combined with spared perceptual and conceptual abilities, indicating specific involvement in lexical access (see Gow, 2012, for a review). Moreover, Marinkovic et al. (2012) estimated the source of the theta power difference between visually presented words and pseudowords in their MEG data to be in the left temporal cortex (although this source extended into the left inferior frontal lobe).

Previous fMRI work on word learning has accordingly demonstrated an increased BOLD signal in left pMTG involvement after consolidation (Takashima, Bakker, van Hell, Janzen, & McQueen, 2014). In this study, participants learned a set of novel spoken words and performed a recognition task immediately after learning as well as 24 hr later. After the consolidation period, left pMTG activation in response to correctly recognized novel words increased relative to the response observed in the immediate scanning session. Postconsolidation functional connectivity between the auditory cortex and this MTG region was further enhanced for those participants who exhibited stronger behavioral evidence of lexical integration. These data, as well as those of Takashima, Bakker, van Hell, Janzen, and McQueen (2017), who examined consolidation of newly learned words after a 1-week delay, are in line with the hypothesis that lexical storage in the left pMTG develops during offline consolidation.

The current study was designed to test the hypothesis that the consolidation effect we previously observed in the theta band is driven by an increase in left pMTG involvement, which would support the CLS claim that consolidation of novel words facilitates the lexicalization of their representations. As in Bakker et al. (2015), participants were trained on written novel and existing words on 2 consecutive days, after which MEG responses to the learned words plus an untrained set were recorded during a semantic decision task. Behavioral measures of lexical competition and semantic priming were obtained to assess the functional integration of novel words into the existing lexicon. The difference in theta power elicited by novel versus existing words was computed at each level of training. We then used a beamformer approach (Gross et al., 2001) to identify the most likely neural generators of these lexicality effects and asked whether the change between recent and remote words could be localized to the left pMTG. Because we previously observed additional, less robust consolidation-dependent changes in beta (16–21 Hz) power (Bakker et al., 2015), lexicality effects in this frequency band were also investigated.

METHODS

Participants

Twenty-nine right-handed (as assessed by an abridged version of the Edinburgh Handedness Inventory;

Oldfield, 1971) native speakers of Dutch (eight men), aged 18–35 years (mean = 23 years), participated in the experiment in return for course credit or monetary compensation. Participants had no history of neurological or language-related disorders and reported having normal or corrected-to-normal vision and hearing. One male participant and one female participant were removed from the MEG analyses because of excessive movement, and one female participant was removed because of large eye-movement-related artifacts. One female participant was removed from all analyses because of experimenter error.

Design

Participants were trained on two different sets of novel and existing words, one set on each of 2 consecutive days (see Figure 1 for an overview of tasks). Immediately after the second training session, participants performed a semantic decision task in the MEG scanner. This task contained the trained novel and existing words from the first session (remote condition), the trained novel and existing words from the second session (recent condition), and a set of novel and existing words that were not part of the trained set (untrained condition). This design allowed us to compare the effect of consolidation on the difference between novel and existing words within a single recording session, using the existing words as a baseline for each novel condition to control for processes related to episodic rather than lexical retrieval. Finally, two behavioral tasks measured lexical competition between novel and existing words (semantic decision on the base words) and semantic priming from novel to existing words (primed lexical decision). All materials were presented in the visual modality only.

Materials

The materials largely overlapped with those used by Bakker et al. (2015), but for the purpose of the semantic decision task on the base words (see Procedure section), some items were adapted such that the base words of half of the novel words in each list referred to natural

objects and half referred to artifacts. Four lists of 20 novel words (see Table 1) of four to seven letters (mean = 5.2 letters) were derived from Dutch words by substituting one letter, for example, “pamat” from “patat” (chips). Base words had no or few orthographic neighbors (mean = 2.7) and had a frequency of 1–112 per million (mean = 12.7 per million) in the CELEX database (Baayen, Piepenbrock, & Gulikers, 1995). The substituted letter was in the first position in 17 words, between the second and penultimate positions in 45 words, and in the last position in 18 words. The four lists were matched on number of neighbors, word length, and frequency of the base words.

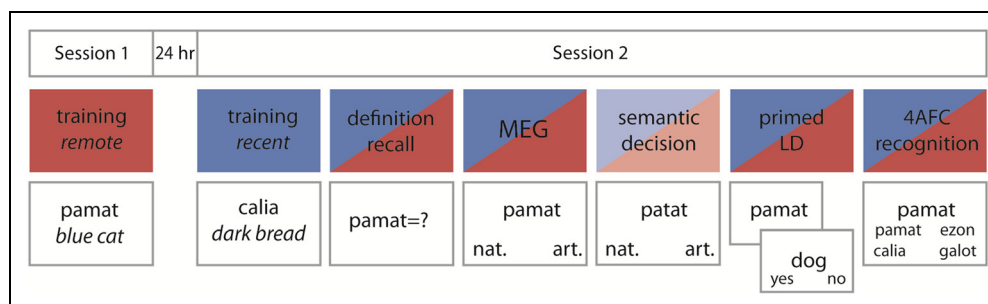
Two lists of 20 definitions were created to provide the novel words’ meanings, in part based on Tamminen and Gaskell (2013) and largely identical to those used by Bakker et al. (2015). Each definition consisted of an existing object category paired with two distinguishing features, for example, “A cat that has stripes and is bluish gray,” and thus described a novel subcategory of an existing concept.

For each participant, two of the four lists of novel words and both lists of definitions served as the to-be-learned material, one in each of two learning sessions (recent and remote). The pairing of novel words and definitions was randomized for each participant. The third list of novel words was used as the untrained condition in the MEG task, and the base words of the fourth list served as the untrained condition in the semantic decision task. The pairing of lists and tasks/conditions was rotated across participants.

Three lists of 20 existing Dutch words (see Table 2) of four to eight letters (mean = 5.8 letters) with a frequency of 1–195 per million (mean = 32.7 per million) were created and matched on frequency and length. Each existing word was presented with a realistic definition (e.g., “lemon: a yellow, sour-tasting fruit”). Each participant saw two of the three lists of existing words and definitions, one in each of the two learning sessions. The third list served as the untrained existing condition in the MEG task.

For the purpose of the behavioral primed lexical decision task, three semantically related existing Dutch target words were selected for each novel word meaning’s category label

Figure 1. Schematic overview of tasks. The bottom row gives an abbreviated example of a trial. Participants learned a set of novel and existing words in Session 1 (remote) and a second set of novel and existing words 24 hr later in Session 2 (recent). Tests in Session 2 included both the recent (indicated by blue) and remote (indicated by red) sets as well



as a set of untrained (novel and existing) words in the MEG task. The semantic decision task was performed on the base words from which the novel words were derived (indicated by lighter colors). LD = lexical decision; nat. = natural; art. = artifact.

Table 1. Novel Word Stimuli and Their Existing Dutch Base Words

<i>Novel</i>	<i>Base</i>	<i>Translation</i>	<i>Novel</i>	<i>Base</i>	<i>Translation</i>
<i>List 1</i>			<i>List 2</i>		
celmo	cello	cello	eglo	iglo	igloo
ablas	atlas	atlas	radak	radar	radar
hile	file	traffic jam	waraf	karaf	carafe
alcum	album	album	abulet	amulet	amulet
dokane	douane	customs	indet	index	index
alara	alarm	alarm	asaalt	asfalt	asfalt
mobot	robot	robot	trefe	trede	step
saltris	salaris	salary	niald	naald	needle
catera	camera	camera	meibel	meubel	item of furniture
tadi	taxi	taxi	fleb	fles	bottle
nobra	cobra	cobra	lepia	lepra	lepra
frec	fret	ferret	prema	poema	puma
uzer	uier	udder	sprug	spuug	spit
porin	porie	pore	relma	reuma	rheumatism
lagine	lawine	avalanche	astia	astma	asthma
halik	havik	hawk	puzil	pupil	pupil
vidus	virus	virus	stelet	skelet	skeleton
ziloer	zilver	silver	ramijn	ravijn	ravine
alimaat	klimaat	climate	okrel	oksel	armpit
ratuur	natuur	nature	gole	golf	wave
<i>List 3</i>			<i>List 4</i>		
tosto	tosti	toast	bumier	bumper	bumper
pamat	patat	chips	kiosa	kiosk	kiosk
kohma	komma	comma	merro	metro	metro
assel	asiel	asylum/ shelter	mossee	moskee	mosque
keno	kano	canoo	palaar	pilaar	pillar
fiche	fiche	chip	pialm	psalm	psalm
jenu	menu	menu	oriel	orgel	organ
ofera	opera	opera	pontein	fontein	fountain
hemb	hemd	vest	perzon	perron	platform
teno	tent	tent	kantoog	kantoor	office
elane	eland	moose	ezone	ozon	ozone
calia	cavia	guinea pig	fnoe	gnoe	gnu
ananak	ananas	pineapple	inoor	ivoor	ivory
elster	ekster	magpie	lamboe	bamboe	bamboo

Table 1. (continued)

<i>Novel</i>	<i>Base</i>	<i>Translation</i>	<i>Novel</i>	<i>Base</i>	<i>Translation</i>
gjord	fjord	fiord	galot	galop	gallop
arwt	erwt	pea	perdik	perzik	peach
taroe	tarwe	wheat	nund	rund	cow
vitroen	citroen	lemon	moerak	moeras	swamp
maverie	materie	matter	ozel	ezel	donkey
winc	wind	wind	riviet	rivier	river

(e.g., DOG for “pamat,” if the given definition was a type of cat). As much as possible, targets were taken from a Dutch database of word associations (De Deyne & Storms, 2008) or, in case the prime word was unavailable in that database, from the Florida Free Association Norms (Nelson, McEvoy, & Schreiber, 1998). Target words were composed of 3–10 letters (mean = 5.2 letters), with a frequency of 1–1084 per million (mean = 71.7 per million). The two lists of novel word meanings were matched for target length and frequency. No target words occurred in any of the definitions or as a base word of one of the novel words. Three unrelated prime–target pairs were created for each meaning by shuffling the list of target words.

Procedure

Training and Memory Tests

The training and memory test procedures were identical to Bakker et al. (2015). Briefly, training consisted of a round of exposure to each word–definition pair, followed by two rounds of a series of four training blocks: (1) two-alternative forced-choice word–definition matching where definitions were the cues and words were the choices, three trials for each item; (2) two-alternative forced-choice 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. All responses were typed on the computer. Feedback was provided on each trial. In total, participants received 17 exposures of each word–definition pair. Presentation of novel and existing items was mixed, and item order was randomized for each block.

After the training phase in the second session, participants performed a definition recall block without feedback, in which the learned novel and existing words from both training sessions served as cues to recall their meanings. This block was included to reactivate the remote condition and to minimize perceptual effects of recency of exposure as well as to measure memory for the remote set without intervening exposure. Given that this task is highly demanding, we also administered a

Table 2. Existing Word Stimuli

<i>List 1</i>		<i>List 2</i>		<i>List 3</i>	
<i>Stimulus</i>	<i>Translation</i>	<i>Stimulus</i>	<i>Translation</i>	<i>Stimulus</i>	<i>Translation</i>
dweil	mop	applaus	applause	reptiel	reptile
vampier	vampire	oorlog	war	borstel	brush
garage	garage	vulkaan	vulcano	tomaat	tomato
sigaar	cigar	monnik	monk	gorilla	gorilla
dokter	doctor	dwerg	midget	bliksem	lightning
herfst	autumn	walvis	whale	tapijt	carpet
hengst	stallion	bijbel	bible	koffie	coffee
pleister	plaster	planeet	planet	oester	oyster
strand	beach	bezem	broom	piano	piano
kreeft	lobster	hotel	hotel	ladder	ladder
suiker	sugar	insect	insect	appel	apple
tijger	tiger	zwaan	swan	druif	grape
duivel	devil	tante	aunt	sneeuw	snow
fiets	bike	ridder	knight	tulp	tulip
slang	snake	kelner	waiter	varken	pig
vlieg	fly	konijn	rabbit	ballet	ballet
dochter	daughter	vinger	finger	banaan	banana
molen	mill	winter	winter	feest	party
keuken	kitchen	slee	sled	winkel	shop
baard	beard	pauw	peacock	zolder	attic

four-alternative forced-choice (4AFC) word–definition matching task at the end of the testing session to confirm that both sets of words could at least still be recognized. The 4AFC task only included the novel words.

MEG Task

The MEG task required participants to make a natural/artifact decision on the 20 novel and 20 existing words from the three conditions: remote, recent, and untrained. Each item was presented five times, for a total of 100 trials per condition. Words were presented at the center of the screen, in black on a gray background. A trial consisted of a fixation screen for 1200 msec, presentation of the word for a randomly jittered period of 1400–1800 msec, and a response prompt for 2000 msec or until the participant responded. Participants pressed one of two buttons, using their left hand, to indicate whether the word referred to a natural or manmade object. For untrained novel objects, which had no meaning, they were instructed to guess. Each trial was followed by a 1200-msec period for blinking.

Semantic Decision on Base Words

The semantic decision task was designed to measure lexical competition from the learned novel words with their existing orthographic neighbors—the base words. Participants made a speeded natural/artifact decision to the base words of the 40 learned novel words as well as to a control set of 20 base words from the fourth list of novel words (i.e., not the list that was on the “untrained” condition in the MEG task). A slower response to base words with novel competitors (e.g., “patat” [chips] when “pamat” has been learned) as compared with base words without any novel competitors is taken to indicate lexical competition and thus integration of the novel word into the lexicon. A set of 80 filler items was included to distract participants from the relation between the base words and the learned novel words. Half of the items in each condition required a “natural” response; and half, an “artifact” response. Trials consisted of a 500-msec fixation cross and a 500-msec blank screen, followed by presentation of the stimulus word for 2000 msec or until button press. Responses were measured until 1500 msec after target onset. Participants used their left and right

index fingers to indicate their responses, with the allocation of response buttons being counterbalanced across participants.

Primed Lexical Decision Task

The primed lexical decision task measured the ability of novel words to speed up responses to semantically related existing words, indicating their semantic integration into the lexicon. Each trained novel word was presented as a prime once with each of three semantically related targets and once with each of three unrelated targets. In addition, each trained word was presented six times as a prime with a different nonword target, derived from unrelated existing target words by substitution of one letter. Thus, there were 240 nonword and 240 word response trials, for a total of 480. A trial consisted of a 500-msec fixation screen and presentation of the prime in lower case letters for 250 msec, followed by an interval of a blank screen for 250 msec and presentation of the target in capital letters for 1500 msec or until button press. Participants were instructed to indicate as fast as possible whether the target word was a real Dutch word or not by pressing a button under their left index finger for “no” or their right index finger for “yes.”

MEG Acquisition and Analysis

MEG data were acquired from 275 axial gradiometers (CTF VSG MedTech) digitized at a sampling frequency of 1200 Hz, after analog low-pass filtering at 300 Hz. Head position was tracked in real time using two coils attached to the ear plugs and one placed at the nasion. Position of the head was readjusted relative to the start of the recording during breaks. Eye movements were recorded using the SR Research Eyelink 1000 on the left eye.

Data analysis was performed using FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011). The raw data were segmented into epochs containing the baseline period and the word presentation period (1400 msec prestimulus to 1200 msec poststimulus). Trials containing muscle artifacts, a head position that was more than 6 mm displaced from the starting position, and SQUID jumps were removed (4%). Heartbeat and eye movement components were subsequently identified using independent component analysis and removed from the data. Consistently noisy channels were also removed (the same three channels for all participants and a fourth channel for one participant).

For sensor level analysis, synthetic planar gradients were computed to facilitate topographical interpretation when comparing across participants (Bastiaansen & Knösche, 2000). Time–frequency representations of power were estimated for frequencies between 4 and 30 Hz using a sliding window of 500 msec in steps of 50 msec, multiplied with a Hanning taper. Normalized differences of power between novel and existing words $[(\text{novel} - \text{existing}) / (\text{novel} + \text{existing})]$ were computed for each level of train-

ing (untrained, recent, and remote). Normalizing minimizes biases based on potential overall power differences between conditions, for instance, due to a difference in recency of exposure, number of trials, or presence of artifacts. As in Bakker et al. (2015), a window of 500–600 msec was selected for statistical analysis, which due to the length of the sliding window, is influenced by data between 250 and 850 msec. Power was averaged across left temporal channels (see Figure 4A), based on the topography of the theta effect in Bakker et al.

A Dynamic Imaging of Coherent Sources scalar beam-forming approach was used to estimate the sources of theta oscillations (Gross et al., 2001). T1-weighted anatomical MRIs with 1-mm isotropic voxels were obtained on a 1.5-T Siemens (Erlangen, Germany) Avanto scanner for all participants and used to construct realistic volume conduction models as well as individual volumetric source models. The latter were based on a regular 3-D grid with a 1-cm resolution, created from the Montreal Neurological Institute template brain, giving 2982 grid points within the brain. The participants’ scans were normalized to the Montreal Neurological Institute template brain, and the inverse transformation was applied to the template grid, such that a given grid point location in a participant corresponded to the same grid point location in volumetrically normalized space.

For source localization of theta and beta effects, data from a 300- to 800-msec time window were multiplied with a Hanning taper (leading to frequency smoothing of ~ 2 Hz) and transformed to the frequency domain using a fast Fourier transform. This time window was chosen to be centered around the peaks of the channel level effects observed in Bakker et al. (2015) and to contain at least two cycles of the frequency of interest. For the theta band, a center frequency of 6 Hz was used, and for the beta band, a center frequency of 18 Hz was used. We used a common spatial filter across conditions to obtain a power estimate for each grid point and condition that is unbiased by potential differences (such as noise level or number of trials) between conditions. This was achieved by averaging the data across all conditions and creating a condition-averaged cross-spectral density (CSD) matrix. From the CSD and the leadfield (the forward model of sensor distribution of cortical sources), we constructed a common spatial filter. This filter was then applied to the CSD matrix of each condition separately, resulting in a power estimate for each grid point and condition. The normalized difference between novel and existing words was then computed for each level of training.

The ROI analysis of the left pTMG used a mask created by cutting a straight line across the left MTG region of the automated anatomical labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002) at the middle y value along the anterior–posterior axis (see Figure 2). The AAL atlas was interpolated to the template grid, and each participant’s theta power estimates for the grid points corresponding

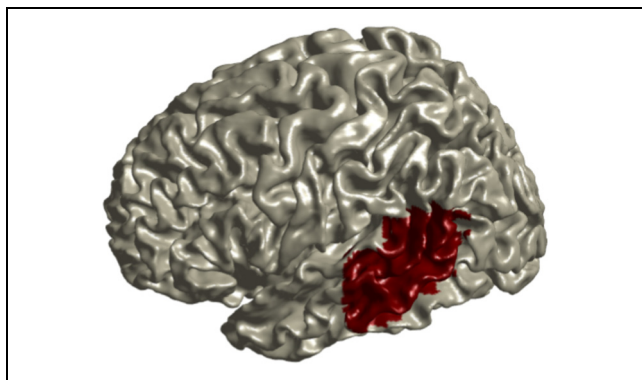


Figure 2. Left posterior MTG mask used for ROI analysis, created by cutting a straight line across the left MTG region of the AAL atlas (Tzourio-Mazoyer et al., 2002) at the middle y value along the anterior–posterior axis.

to the left pMTG mask were extracted. The averages were entered into a repeated-measures ANOVA.

To establish whether any theta effects were driven mainly by induced or evoked activity, we repeated our main statistical analysis on the phase-locked portion of the response. To compute the theta power of the evoked response, we averaged the single-trial Fourier coefficients and took the magnitude squared of the result. Given that Fourier transformation is a linear operation, this procedure is mathematically equivalent to single trial averaging in the time domain, followed by Fourier transformation. To compare the evoked theta power across the three conditions, we calculated the theta-band spectral power of the condition-specific evoked response in the 300- to 800-msec time window. We then performed a repeated-measures ANOVA on the mean theta power values, as before.

RESULTS

Behavioral Results

Training and Memory Performance

In the last block of training, participants could produce the correct category name (e.g., “cat”) when cued by a novel word in 97.1% ($\pm 5\%$) of items on Day 1 and 97.7% ($\pm 4\%$) on Day 2. The number of definition features given for novel words was 87.8% ($\pm 10.3\%$) on Day 1 and 89.7% ($\pm 10.4\%$) on Day 2. Thus, participants successfully learned the novel word meanings and performed similarly on both sets.

In the definition recall task without feedback, presented immediately after the training procedure on Day 2, 94.1% ($\pm 7.6\%$) of the features were recalled in the novel recent condition; and 71% ($\pm 23.3\%$), in the novel remote condition. The correct category (e.g., “cat”) was given in 95.7% ($\pm 6.8\%$) of the novel recent words and 72.5% ($\pm 20.8\%$) of the novel remote words. As expected, performance for existing words was at ceiling.

Recognition of novel words when cued by their definitions in the 4AFC task at the end of the second session was successful for 75% ($\pm 17.6\%$) of the recent words and 70.4% ($\pm 16.2\%$) of the remote words. This level of performance suggests that, although some forgetting had occurred, the meanings of most words of both sets were still retrievable at the time of testing.

MEG Task

The novel untrained condition was excluded from behavioral analysis of the semantic decision task performed during the MEG recording, as these words were meaningless and participants were instructed to give a random response to them. Overall accuracy across the other conditions was 88.4% (recent novel: 90.6%, remote novel: 84.8%; recent existing: 88%, remote existing: 88.4%).¹ After the procedure taken in our previous EEG study (Bakker et al., 2015), errors and RTs above or below 1.5 SDs from the mean were removed for RT analysis (19.1%). A Day \times Lexicality ANOVA did not reveal an interaction or main effects (all $ps > .4$).

Semantic Priming

Lexical decision accuracy in the priming task was 93.6%. RTs were analyzed using an ANOVA with factors Relatedness (related/unrelated prime) and Day (recent/remote). Errors and RTs below or above 1.5 SDs from the mean were removed (14.4%). The RT analysis did not reveal a main effect of Relatedness (i.e., an overall priming effect; $F(1, 27) = 0.25, p = .621$) or an effect of Day ($F(1, 27) = 0.148, p = .704$). The interaction, however, was significant, reflecting a change in the direction of the priming effect ($F(1, 27) = 4.297, p = .048$). In the recent condition, a numerical slowing down (8 msec) was observed for related prime–target pairs ($t(27) = 1.7, p = .101$, evaluated at $\alpha = .025$ to correct for multiple comparisons following the sequential Holm–Bonferroni [H-B] method; Holm, 1979). In the remote condition, the expected facilitation occurred (5 msec) but did not reach significance ($t(27) = 1.214, p = .235$, H-B $\alpha = .05$). This pattern suggests that the novel words’ ability to prime existing words did increase with consolidation but did not (yet) reach the point at which they significantly facilitated recognition (see Figure 3A).

Lexical Competition

Lexical competition between the novel words and the base words from which they had been derived (e.g., “patat,” chips, the base word of “pamat”) was tested with a one-way ANOVA on the three conditions: remote (novel neighbor learned on Day 1), recent (novel neighbor learned on Day 2), and untrained (no novel neighbor). Accuracy was 87.3%, and errors and RTs below or above 1.5 SDs from the mean were removed from the RT analysis

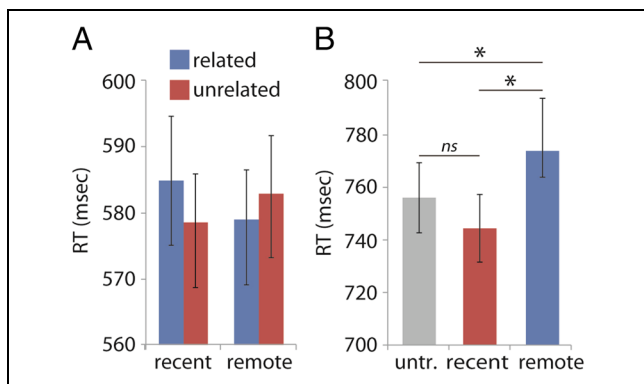


Figure 3. Behavioral integration results. (A) RTs to related and unrelated prime–target pairs for the remote and recent conditions in the primed lexical decision task. Error bars denote standard errors. (B) RTs to the existing base words of untrained (untr.), recent, and remote novel words in the semantic decision task. Error bars denote standard errors.

(21.7%). ANOVA revealed a main effect of Condition ($F(2, 54) = 4.478, p = .016$). Responses in the remote condition were 18 msec slower than those in the untrained condition, indicating that novel words (e.g., “pamat”) entered into lexical competition with their existing neighbors (e.g., “patat”; $t(27) = 2.332, p = .027$, marginally significant at $H-B \alpha = .025$). In contrast, there was no sign of competition in the recent condition ($t(27) = 1.078, p = .291, H-B \alpha = .05$). The difference between the two effects (remote–untrained vs. recent–untrained) was significant ($t(27) = 2.693, p = .012$; see Figure 3B).

MEG Results

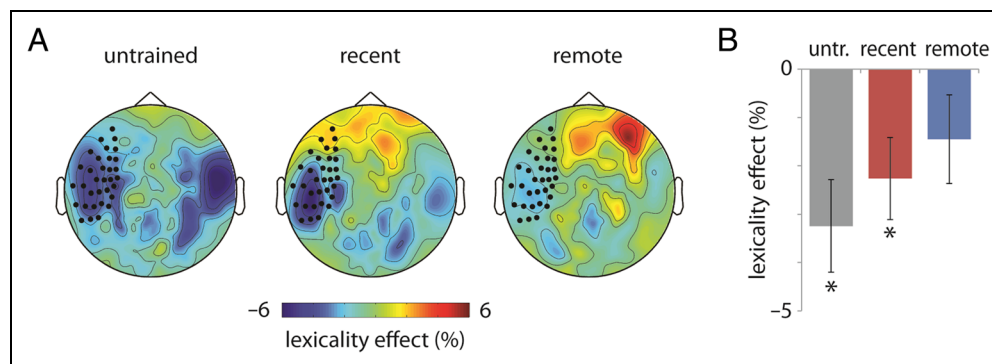
The change over time in channel-level theta power (4–8 Hz) in the 500- to 600-msec time window over left fronto-temporal channels was analyzed with a one-way ANOVA on the normalized differences between novel and existing words in each of the three conditions, as in Bakker et al. (2015). This analysis replicated the pattern observed in that study, although the main effect of

Condition was nonsignificant ($F(2, 48) = 1.265, p = .292$). One-sample t tests for each of the three conditions confirmed that untrained novel words elicited lower theta power than existing words ($t(24) = 3.423, p = .002, H-B \alpha = .017$). This lexicity effect remained significant for recent words ($t(24) = 2.660, p = .014, H-B \alpha = .025$) but was absent in the remote condition ($t(24) = 1.555, p = .133, H-B \alpha = .05$; see Figure 4).

Our main hypothesis was that theta lexicity effects in the left pMTG decrease with consolidation. We therefore extracted the power estimates for the grid points corresponding to the anatomical left pMTG² for each condition and performed a one-way repeated-measures ANOVA on the regional averages (see Figure 5A). This analysis revealed a significant change in the magnitude of the lexicity effect across conditions ($F(2, 48) = 3.832, p = .029$). One-sample t tests on the normalized differences per condition showed that both untrained and recent novel words elicited lower theta responses in the pMTG than existing words (untrained: $t(24) = 4.35, p < .001, H-B \alpha = .017$; recent: $t(24) = 3.457, p = .002, H-B \alpha = .025$). In the remote condition, this lexicity effect was no longer significant ($t(24) = 0.286, p = .777, H-B \alpha = .05$). To quantify the change in magnitude of lexicity effects, we then compared the novel–existing difference for untrained words with the novel–existing difference for recent words. This difference was not reliable ($t(24) = 0.424, p = .676, H-B \alpha = .05$), suggesting that training alone did not significantly reduce the lexicity effect. Comparing the differences for recent and remote words revealed a marginally significant decrease in lexicity effects ($t(24) = 2.258, p = .033, H-B \alpha = .025$), indicating that the interaction effect was largely driven by a difference between the recent and remote conditions.

To control for the possibility that the pMTG effects resulted from bleeding of activation from adjacent areas, the main one-way ANOVA on the normalized differences was repeated in the left superior temporal gyrus (STG) and inferior temporal gyrus (ITG), angular gyrus, supra-marginal gyrus, and inferior parietal lobule (as defined in the AAL atlas; Tzourio-Mazoyer et al., 2002). None of these

Figure 4. Lexicity effects (novel – existing / novel + existing) in the theta band (4–8 Hz) for untrained (untr.), recent, and remote words, averaged across participants. (A) Sensor topography of the average lexicity effect, averaged across 500–600 msec. Blue indicates a negative difference in power (less synchronization for novel words than existing words). (B) Lexicity effects averaged across the left fronto-temporal channels highlighted in A, based on Bakker et al. (2015).



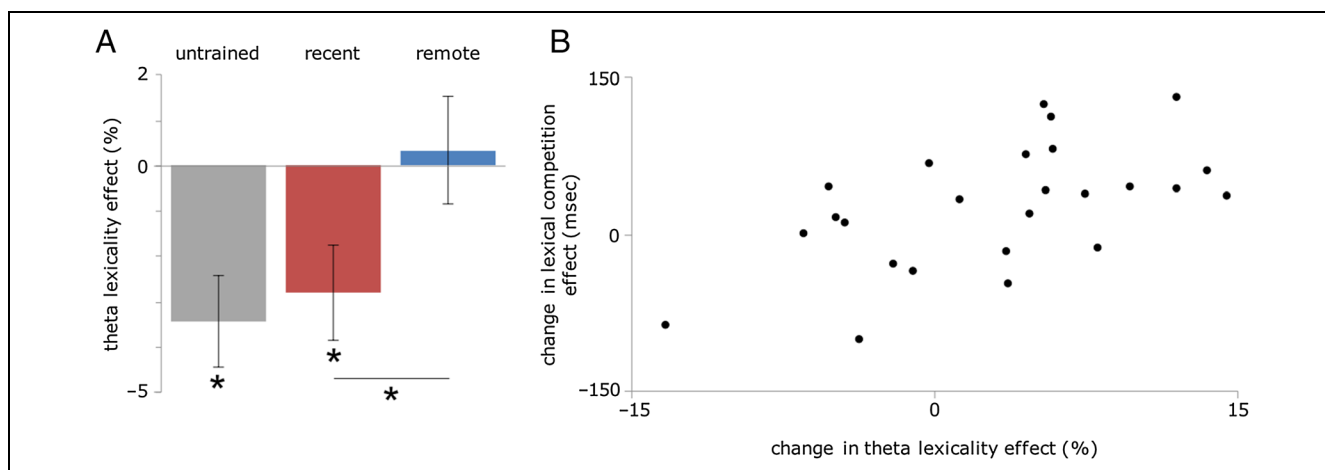


Figure 5. (A) Lexicality effects (novel – existing / novel + existing) in the theta band (4–8 Hz) averaged across the left pMTG ROI at source level. Error bars denote standard error. (B) Correlation between the decrease in lexicality effects in the left pMTG and the increase in competition effects (difference between remote and recent effects) after consolidation.

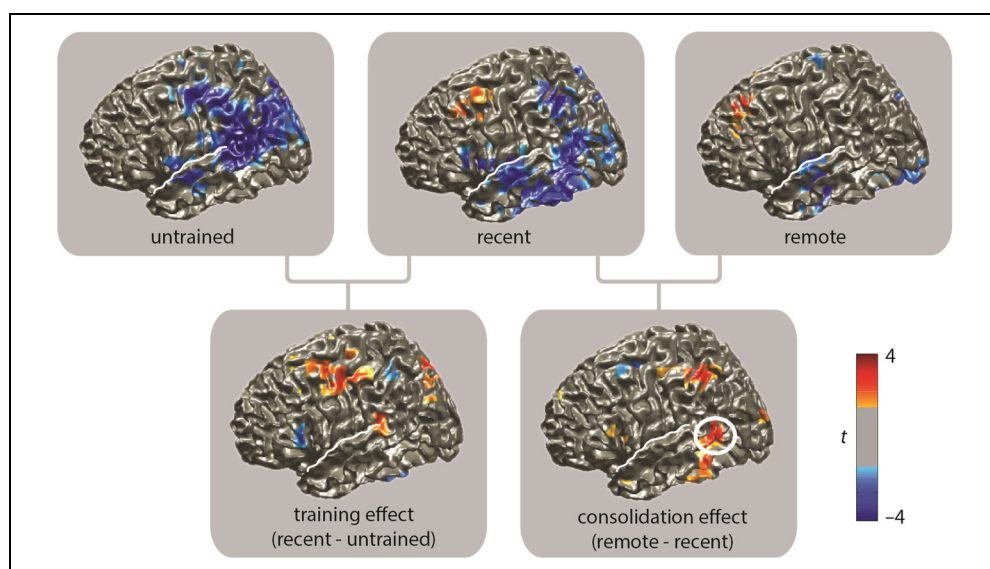
regions exhibited a change in lexicality effects across conditions (all p s > .069), confirming that the effect is specific to the MTG. Second, we investigated whether the observed theta effect could be explained by time-locked (e.g., N400-related) activity. We did not observe a change in lexicality effects within the evoked part of the activity ($F(2, 48) = 1.869, p = .165$), suggesting that the effect was driven at least predominantly by induced activity.

To investigate the relation between theta power and behavioral integration effects, we computed the correlation between the magnitude of the theta lexicality effect in both learned conditions and the magnitude of the behavioral priming and competition effects. No correlations were observed between the theta lexicality effect and the priming effect for remote or recent words or between the

theta lexicality effect and the competition effect for remote or recent words (all p s > .5). However, the degree to which the theta lexicality effect decreased after consolidation (remote lexicality effect vs. recent lexicality effect) was correlated with the increase in competition effects after consolidation (remote competition effect vs. recent competition effect; $r(23) = .56, p < .001$). This suggests that a more word-like theta response in the remote condition is related to the emergence of competition effects from those words (see Figure 5B). No correlation was observed between the change in theta lexicality effects and the change in priming effects, possibly because the priming effect remained weak even in the remote condition (see Figure 3).

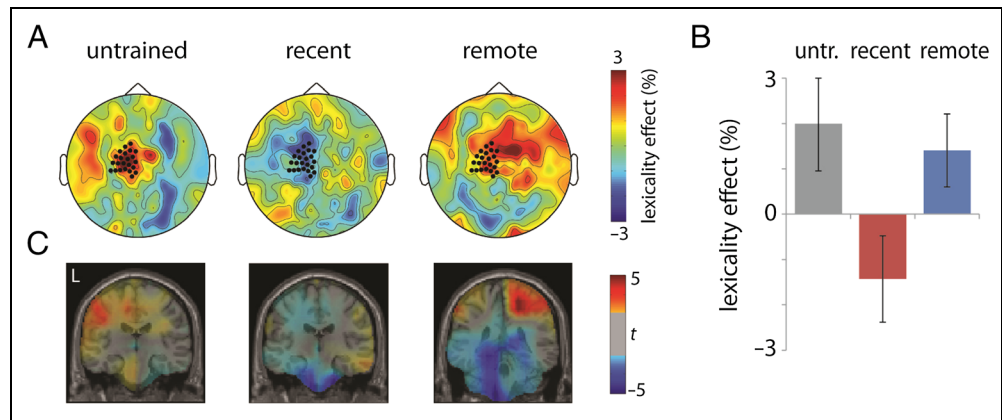
Given our strong prior hypothesis regarding the left pMTG, we restricted ROI analysis and correlations with

Figure 6. Estimated source activity for the lexicality effects, computed for 4–8 Hz and 300–800 msec. Uncorrected parametric t values (thresholded at $p = .05$) are plotted to illustrate the most consistent source estimates. (Note that the use of t values here is merely a way to visually illustrate the relative consistency of the effects across different areas, and no conclusions about the significance of these effects can be drawn from this figure.) The white line indicates the location of the Sylvian fissure for orientation purposes. The top row shows the lexicality effect per condition as a T statistic (novel-existing),



with blue indicating lower theta power for novel words as compared with existing words and red indicating higher theta power for novel than existing words. The bottom left shows the change in magnitude of the lexicality effect between the untrained and recent conditions. Red colors signify a decrease of the lexicality effect in the recent condition, that is, an effect of training. The bottom right shows the change in magnitude of the lexicality effect between the recent and remote conditions. Red here indicates a decrease of the lexicality effect in the remote condition, that is, a consolidation effect. The white circle indicates the location of the largest effect, which is estimated to be in the posterior MTG.

Figure 7. Lexicality effects (novel – existing/novel + existing) in the beta band (16–20 Hz) for untrained (untr.), recent, and remote words. Red indicates a positive difference in power (more synchronization for novel than existing words); blue, the opposite. (A) Topography of the lexicality effect, averaged across 300–500 msec. (B) Lexicality effects averaged across the left fronto-temporal channels highlighted in A, based on Bakker et al. (2015).



(C) Estimated sources of beta lexicality effects. Colors follow the same conceptual interpretation as in A, but t values (thresholded at $p = .05$) are plotted to illustrate the most reliable source estimates.

behavioral effects to this region. However, to illustrate the overall spatial pattern of lexicality effects in the theta band, Figure 6 shows a surface rendering of the estimated source activity of the difference between novel and existing words in each condition, expressed as a T statistic. Note that these values are uncorrected and serve only to illustrate the topography of the effect, not as a test of significance. Furthermore, the spatial resolution of MEG is limited, and the anatomical location of sources is therefore only an approximation. Untrained words exhibited the strongest lexicality effect in the region of the left STG and MTG, extending medially into the medial-temporal lobe and dorsally into the angular gyrus, supramarginal gyrus, and precentral and postcentral gyrus as well as in the right medial-temporal lobe. In the recent condition, the largest difference was estimated to be around the ITG and fusiform gyrus, MTG, and anterior STG, extending into the inferior frontal gyrus. The difference in theta power also seems to be reflected in the region of the inferior parietal lobule and postcentral gyrus. The peak voxel for the smaller lexicality effect in the remote condition was estimated to be in the left fusiform gyrus, and this source extended into the medial-temporal lobe and anterior part of the ITG. The right fusiform gyrus also exhibited a lexicality effect. As illustrated at the bottom left of Figure 6, training did not reduce the lexicality effect in the left pMTG. In contrast, comparison of the effects in the remote versus recent conditions showed that lexicality effects after consolidation were most reduced (the highest t values were observed) in the posterior part of the left MTG, consistent with the MTG ROI analysis (bottom right of Figure 6). A second peak was observed in the left inferior parietal lobule.

Unlike in our previous EEG data (Bakker et al., 2015), we did not observe a clear consolidation effect in the lower beta band (Figure 7). On the basis of the EEG findings, we analyzed 16- to 20-Hz activity in a 300- to 500-msec window over left central channels. In line with the earlier findings, this revealed numerically weaker beta desynchronization (i.e., higher beta power) for untrained novel

words compared with existing words ($t(24) = 2.072, p = .049, H-B \alpha = .017$). The source of this effect (at ~ 18 Hz) was localized most strongly to the left postcentral gyrus. However, there was a numerical effect in the opposite direction for the recent condition ($t(24) = 1.591, p = .125, H-B \alpha = .025$) and a numerical difference in the same direction for the remote condition ($t(24) = 1.695, p = .103, H-B \alpha = .05$). The estimated source of the effect for remote words was in the right postcentral gyrus.

DISCUSSION

The current study tested the hypothesis that the development of lexical representations of novel words causes a more word-like pattern of theta synchronization in the left pMTG after consolidation. As expected, the sensor level data show that untrained novel words (i.e., pseudo-words) elicited lower theta synchronization than existing words in the left fronto-temporal sensors. The estimated sources of this effect comprised a mostly left-lateralized network of temporal and parietal regions. ROI analysis of the pMTG revealed that training of novel words only before test (recent condition) did not reduce the difference between theta responses to novel and existing words. In contrast, the lexicality effect in the pMTG was significantly reduced for responses to words learned 24 hr previously (remote condition), which no longer differed from responses to existing words. Comparing the magnitude of the lexicality effect for recent versus remote words further revealed that the largest decrease occurred in the pMTG (Figure 6), confirming the hypothesis that this region supports the formation and integration of lexical representations for novel words. Although the limited spatial resolution of MEG prohibits detailed conclusions about the anatomical location of sources, and several language-related areas may contribute to this effect (such as the STG, ITG, and inferior parietal lobule), the whole-brain analysis suggests that the largest decrease occurred in the posterior part of the left MTG.

These results replicate our earlier observation of decreased theta lexicality effects after consolidation (Bakker et al., 2015) and link this theta effect to fMRI data implicating the left MTG (and, in particular, its posterior half) in novel word consolidation (Takashima et al., 2014, 2017). The posterior MTG has been proposed to function as a lexical “association area,” which maps between word-form representations and semantic information distributed throughout the cortex (Gow, 2012; Lau et al., 2008; Hickok & Poeppel, 2004, 2007). Theta synchronization may be one of the mechanisms by which these widely distributed representations are simultaneously activated, enabling them to be accessed as a single lexical item. On this view, the activation of such a coherent word-specific network bound together by the pMTG would lead to local theta synchronization, producing the scalp-level power increase over left temporal and frontal channels that was observed here and in other studies (Bakker et al., 2015; Marinkovic et al., 2012; Bastiaansen et al., 2005, 2008; Krause et al., 2006). The degree to which form- and meaning-related information for a given word is available and accessible via the pMTG thus predicts the level of theta power during recognition of that word. Training a novel word with its meaning initiates changes in the pMTG, but only after a consolidation period are the new connections strong enough to elicit word-like oscillatory responses. It remains to be determined if, for each novel word, a new representation is formed in the pMTG that is linked to word-form and semantic (and syntactic) representations of that word (e.g., a lemma representation; see, e.g., Levelt, Roelofs, & Meyer, 1999). Alternatively, the pMTG may serve to connect the different types of lexical representations located elsewhere without the formation of a new representation such as a lemma. On either view, however, what is consolidated is the way in which the novel word is integrated, not only with knowledge about that word (e.g., about its form or meaning) but also with knowledge about other words.

The consolidation of lexical representations has been claimed to underlie the emergence of behavioral evidence of interaction between novel and existing words, such as lexical competition (Bakker et al., 2014; Dumay & Gaskell, 2007, 2012; Gaskell & Dumay, 2003) and semantic priming (van der Ven et al., 2015; Tamminen & Gaskell, 2013). In line with these studies, the present data revealed a competition effect between novel words and their existing orthographic neighbors in a semantic decision task. This competition effect was found for novel words learned the previous day, but not for words learned immediately before test. Such delayed competition effects have generally been interpreted as evidence for the transformation of initially episodic memory traces toward neocortically integrated lexical representations (Davis & Gaskell, 2009). On the basis of the behavioral data alone, however, it is difficult to exclude the possibility that consolidation of the episodic trace itself may increase its accessibility and

enable competition effects. Here, we show that the increase in competition after consolidation correlated with the decrease in pMTG theta lexicality effects, suggesting that novel words that elicited more word-like theta responses were better integrated in the existing lexicon. This novel finding provides further empirical support for the assumption that novel words’ ability to interact with existing words relies on the formation of lexical representations and/or the links between them, rather than the strengthening of an episodic memory trace.

Given that competition is generally assumed to occur at the modality-specific lexeme level (see Bakker et al., 2015, for a discussion), a question that arises from this finding is how the pMTG contributes to the competition process itself. One potential explanation is that the pMTG lemma representation itself does not play a direct role in the competition process, and the correlation arises from the fact that the lexicality effect on pMTG theta power and the behavioral competition effect both result from the same general consolidation process that transforms episodic memory traces into distributed neocortical representations. Alternatively, the availability of a lemma representation may strengthen competition indirectly through top-down activation of lexemes and/or sublexical representations. Distinguishing between these explanations is beyond the scope of the current design but remains an interesting question for future investigations.

The current data are consistent with the CLS claim that neocortical lexical links are established slowly during offline consolidation (Davis & Gaskell, 2009; McClelland et al., 1995). In this framework, the MTG can be seen as gradually taking over the binding function of the hippocampus as novel words are consolidated. However, recent behavioral data suggest that novel words are able to interact with existing words immediately after training when training encourages integration (Coutanche & Thompson-Schill, 2014; Lindsay & Gaskell, 2013; Szmalec, Page, & Duyck, 2012) or when competition is measured with a test that is more sensitive to word-specific competition (Kapnoula, Packard, Gupta, & McMurray, 2015). This may indicate that lexicalization in the pMTG occurs immediately during learning but requires further offline strengthening to produce behavioral effects large enough to be observed with RT methods. This more quantitative neocortical view of lexicalization would be in line with findings that information that is easily related to prior knowledge relies to a much smaller extent on the hippocampus than completely unrelated information, both during encoding and later retrieval (van Kesteren, Ruiters, Fernández, & Henson, 2012; Tse et al., 2007). Future work should attempt to characterize the precise contribution of the hippocampal and neocortical systems in word learning. The current data suggest that theta connectivity between the hippocampus and neocortical structures before and after consolidation may provide a useful measure for this question.

In contrast to Bakker et al. (2015), we did not observe a clear pattern of lexicalization in the lower beta band. Untrained novel words elicited weaker beta desynchronization than existing words, in line with proposals that beta desynchronization reflects retrieval of semantic information (for a review, see Hanslmayr, Staudigl, & Fellner, 2012). Whereas previous semantic beta effects have been localized to the left inferior frontal gyrus (Hanslmayr et al., 2011; Meeuwissen, Takashima, Fernández, & Jensen, 2011), the present effect appeared to be generated by the left postcentral gyrus. This is commensurate with an explanation in terms of motor preparation and response certainty (Alegre et al., 2004). However, the observed pattern is unlikely to reflect only a difference in motor response preparation as participants responded with their left hand, which should produce a right-lateralized effect. It is possible therefore that the beta effect for untrained novel words does reflect a memory-related process. We observed a decreased lexicality effect in the recent condition, but the effect for remote words surprisingly returned to the level of untrained words. The source of this latter effect appeared to be more right lateralized. This pattern is difficult to interpret, but in any case, it does not support a role for beta desynchronization in lexicalization. Future work may be able to shed light on the role of beta desynchronization through the use of a task that does not require any motor response.

In conclusion, the work reported here demonstrates that the left pMTG is associated with a consolidation-dependent development toward more word-like theta responses to novel words. The decrease in the difference in theta power between novel and existing words was found to be correlated with a postconsolidation increase in competition effects, reflecting functional integration of novel words with their existing neighbors. This suggests that theta synchronization enables distributed information to be integrated into lexical representations bound by the pMTG and that the incorporation of novel words into this system benefits from offline consolidation. The current work thus brings together previous observations of behavioral consolidation effects (e.g., Bakker et al., 2014; Tamminen & Gaskell, 2013; Dumay & Gaskell, 2007, 2012; Gaskell & Dumay, 2003), increased pMTG activation in fMRI (Takashima et al., 2014), and more word-like theta responses in EEG after consolidation of novel words (Bakker et al., 2015).

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Notes

- Note that performance on existing words was not perfect because, even with familiar words, it is not always trivial to make a natural/artifact decision, especially under time pressure. Participants differed, for example, in their responses to words such as “monk,” with some reasoning that monks are artifacts because the word refers to a cultural concept, whereas others considered monks natural as they are humans.
- Using the whole left MTG mask from the AAL atlas did not change the pattern or significance level of any of these effects.

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