



Original Articles

The priming of basic combinatory responses in MEG

Esti Blanco-Elorrieta^{a,b}, Victor S. Ferreira^c, Paul Del Prato^a, Liina Pyykkänen^{a,b,d,*}^a Department of Psychology, New York University, New York, NY 10003, USA^b NYUAD Institute, New York University Abu Dhabi, Abu Dhabi, P.O. Box 129188, United Arab Emirates^c Department of Psychology, University of California, San Diego, La Jolla, CA 92093-0109, USA^d Department of Linguistics, New York University, New York, NY 10003, USA

ARTICLE INFO

Keywords:

Priming
Composition
Language production
Magnetoencephalography
Left anterior temporal lobe
Semantics

ABSTRACT

Priming has been a powerful tool for the study of human memory and especially the memory representations relevant for language. However, although it is well established that lexical access can be primed, we do not know exactly what types of computations can be primed above the word level. This work took a neurobiological approach and assessed the ways in which the complex representation of a minimal combinatory phrase, such as *red boat*, can be primed, as evidenced by the spatiotemporal profiles of magnetoencephalography (MEG) signals. Specifically, we built upon recent progress on the neural signatures of phrasal composition and tested whether the brain activities implicated for the basic combination of two words could be primed. In two experiments, MEG was recorded during a picture naming task where the prime trials were designed to replicate previously reported combinatory effects and the target trials to test whether those combinatory effects could be primed. The manipulation of the primes was successful in eliciting larger activity for adjective-noun combinations than single nouns in left anterior temporal and ventromedial prefrontal cortices, replicating prior MEG studies on parallel contrasts. Priming of similarly timed activity was observed during target trials in anterior temporal cortex, but only when the prime and target shared an adjective. No priming in temporal cortex was observed for single word repetition and two control tasks showed that the priming effect was not elicited if the prime pictures were simply viewed but not named. In sum, this work provides evidence that very basic combinatory operations can be primed, with the necessity for some lexical overlap between prime and target suggesting combinatory conceptual, as opposed to syntactic processing. Both our combinatory and priming effects were early, onsetting between 100 and 150 ms after picture onset and thus are likely to reflect the very earliest planning stages of a combinatory message. Thus our findings suggest that at the earliest stages of combinatory planning in production, a combinatory memory representation is formed that affects the planning of a relevantly similar combination on a subsequent trial.

1. Introduction

Language is a combinatory system in which a finite set of basic building blocks serves as the input to a generative engine capable of yielding an infinitude of expressions. Behavioral and brain science has made important advances in our understanding of the cognitive and neurobiological basis of the atomic units of this system – what we represent about them, where they are represented in the brain, and how the cognitive and neural representations of these units relate to other cognitive and neural domains. What is thus far less understood, however, is how neurocognitive mechanisms combine the pieces together into the structures that form more complex linguistic expressions. Here, we present two experiments that use a novel combination of behavioral and neuroscience techniques to gain new insights into the basic

processes that combine words into the next level of complex linguistic structure.

In the behavioral literature, *priming* was one of the most foundational discoveries in the psychology of language (Meyer & Schvaneveldt, 1971; Meyer & Schvaneveldt, 1976), having inspired vast bodies of research characterizing the memory representations relevant for linguistic processing (for review, see Neely, 1991). However, whereas theories of how words are represented have been critically shaped by priming research, the extent to which computations above the word level can be primed remains less understood. That is, whereas the arbitrary relation between the sounds and meanings of lexical items makes it necessary to store words in memory, most combinations of words are formed via a generative procedure, and thus a processor that creates no memory representations for complex structures is at least conceivable.

* Corresponding author at: Departments of Linguistics and Psychology, New York University, New York, NY 10003, USA.
E-mail address: liina.pyykkänen@nyu.edu (L. Pyykkänen).

However, research on sentence processing has shown that at least some aspect of the processing of syntactic structures can be primed (Bock, 1986), especially if the primes and targets share some lexical material (Pickering & Branigan, 1998). The majority of this research has employed language production, showing that the likelihood of a speaker using a certain syntactic structure on a target trial increases if they have been exposed to that structure on a prime trial (for reviews see e.g., Ferreira & Bock, 2006; Pickering & Ferreira, 2008). This effect could reflect processing at many different levels: it could reflect the priming of the particular sequence of combinatory operations required to build the relevant structure, it could reflect a fleeting memory representation of the built structure, or it could reflect the decision processes of the speaker to construct a particular structure as opposed to a competing one. In comprehension, structural priming manifests as reduced processing times for a previously encountered structure. However, compared to production, these effects have been less robust, less straightforward – typically involving ambiguous materials (Branigan, Pickering, & McLean, 2005; Cuetos, Mitchell, & Corely, 1996) – and less independent of lexical overlap (Branigan et al., 2005). Thus it could be that priming in production is, in fact, largely driven by the decision process of choosing a structure, and when this is removed, less priming is observed. This possibility is corroborated by the fact that ambiguity easily brings out priming in comprehension, given that ambiguity resolution also involves a decision process between competing representations. In all, although the structural priming literature clearly shows that priming can be observed above the word level in sentence processing, it does not yet tell us exactly which processing levels can be primed and which cannot.

To approach this question systematically, one would ideally start with the simplest processes that lie closest to lexical access, given that lexical access can be primed. The next step up in the computational hierarchy of language is the basic combinatory operations that build phrases out of words. Could the act of combining *black* with *cat* be primed? If yes, the composition of *black cat* should facilitate the subsequent composition of, say, *brown table*, which is built exactly by the same combinatory rule although none of the same words are involved. In other words, does the application of the abstract adjective + noun rule form a primeable memory representation?

We addressed this basic question by measuring the earliest stages of combinatory processing with magnetoencephalography (MEG), which has already been used to characterize the brain correlates of basic composition across a series of studies (Bemis & Pykkänen, 2011; Bemis & Pykkänen, 2013a; Bemis & Pykkänen, 2013b; Blanco-Elorrieta & Pykkänen, 2016a; Pykkänen, Bemis, & Elorrieta, 2014; Westerlund & Pykkänen, 2014; Westerlund, Kastner, Al Kaabi, & Pykkänen, 2015; Zhang & Pykkänen, 2015). The result relevant for the current study is that both the comprehension and production of adjective-noun combinations engages the left anterior temporal lobe (LATL) and the ventromedial prefrontal cortex (vmPFC) as compared to non-combinatory one or two word stimuli (Bemis & Pykkänen, 2011; Pykkänen et al., 2014). Replications of these results for full sentences (Brennan & Pykkänen, 2012) and other types of two-word phrases (Westerlund et al., 2015) suggest that the effects reflect basic and generalizable combinatory processes. While the same regions have been implicated for both production and comprehension (Bemis & Pykkänen, 2011; Pykkänen et al., 2014), the timing of the activations, unsurprisingly, differs between the two. In comprehension, effects of composition occur first in the LATL at around 200–250 ms, and then in the vmPFC at ~350–400 ms (Bemis & Pykkänen, 2011). However, combinatory effects in the LATL seem to be limited to combinations that are in some sense “simple:” for example, effects of adjectival modification are not seen for head nouns that are conceptually highly specific, suggesting that by 200 ms, the meanings of these nouns have not been sufficiently accessed to allow composition (Pykkänen, 2015; Westerlund & Pykkänen, 2014). Further, there is evidence that the modifications need to be interactive in order for the LATL to engage (Poortman & Pykkänen, 2016; Ziegler & Pykkänen, 2016). LATL effects of







composition have also been reported for compounds, but only for transparent compounds (Brooks & de Garcia, 2015), which is also consistent with prior findings from EEG (MacGregor & Shtyrov, 2013). The vmPFC, on the other hand, does not seem limited to “simple” compositions, in fact, its combinatory role was first characterized for compositions that involve syntax-semantics mismatches (Brennan & Pykkänen, 2008; Brennan & Pykkänen, 2010; Pykkänen, Martin, McElree, & Smart, 2009; Pykkänen & McElree, 2007). Thus in comprehension, the LATL is likely to reflect an early “conceptual sketch pad,” only composing the simplest, most readily accessible meanings, with the vmPFC reflecting a much later stage, perhaps encoding the output of a multi-stage composition process (Pykkänen, 2015). Such vmPFC encoding of the combinatory meaning could then plausibly serve as the starting point in production, in which a message level meaning initiates a series of computations in order to finally produce an articulatory plan. Indeed, vmPFC effects in production have onset as early as 180 ms after picture onset, consistent with this hypothesis (Pykkänen et al., 2014). LATL effects in production have occurred either slightly after or in parallel with vmPFC effects (Pykkänen et al., 2014), suggesting that combinatory activity in the LATL may be relatively time locked to an early time window, whether elicited by production or comprehension. This timeline also fits with the EEG findings of MacGregor and Shtyrov (2013), who found transparent compounds to be processed combinatorially in an early time window (130–160 ms).

Building on this work in our priming paradigm, we first localized combinatory processing during the prime, replicating the prior work (Pykkänen et al., 2014), and then assessed whether activity in the same spatio-temporal location shows priming for a combinatory target when the prime is also combinatory. Importantly, our study is the first to offer not just a measurement of the priming effect on the target but also a measurement of the corresponding, unprimed, activity during the prime. Given that structural priming has been most robust in production, we used picture naming as our main task. Critically, the fine temporal resolution of MEG allowed the measurement of the syntactic and semantic planning stages between picture onset and articulation (Pykkänen et al., 2014), given that the planning of two-word phrases is thought to have entirely completed prior to the onset of articulation and its accompanying motion artifacts (Alario, Costa, & Caramazza, 2002; Meyer, 1996; Schriefers, De Ruiter, & Steigerwald, 1999).

Specifically, on prime trials, subjects named colored objects with adjective-noun combinations (*red boat*) and outlines of objects with single nouns (*boat*). The targets always involved adjective-noun productions, with the priming manipulation consisting of whether the prime and target only shared a structure (Structural: *red boat* – *blue bell*), shared a structure and both words (Full Overlap: *red boat* – *red boat*), or only shared the noun (Lexical: *boat* – *red boat*). Priming of composition was assessed against the last condition, in which the prime was non-combinatory, and the fully overlapping condition was included to safeguard the study against a null result, should there be no purely structure driven priming.

To further characterize the computational stages responsible for possible priming, our design also included two tasks where instead of naming the primes, the primes were more shallowly processed. In the lowest level “View” task, subjects only viewed the prime, allowing us to assess whether any obtained effects were due to the visual properties of the stimuli. In the mid-level “Conceptual” task, we forced subjects to attend to the semantic properties of the primes without actually naming them. This task was intended to diagnose whether priming in target productions may be driven by the comprehension of the complex semantics present in the pictures (i.e., the conceptual combination of a color and an object), a process that has previously been shown to elicit combinatory effects in the vmPFC (Bemis & Pykkänen, 2013). Thus, in all, the study was a $2 \times 3 \times 3$ factorial design crossing Priming (Prime, Target), Prime Task (Naming, Conceptual, View) and Prime Type (FullOverlap, Structural, Lexical), as depicted in Fig. 1A. In addition to the MEG data, speech onset of the target productions was used as a dependent measure.

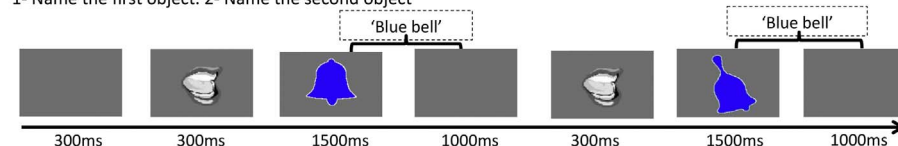
A) Condition design

	Prime Stimulus	Target Stimulus
Full Overlap		
Structural		
Lexical		

B) Trial Structure

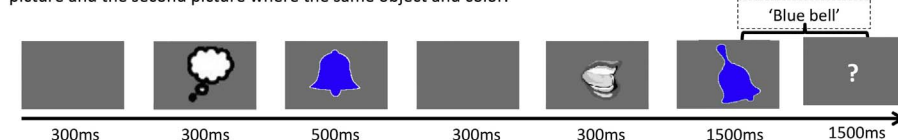
Naming task:

1- Name the first object. 2- Name the second object



Conceptual task:

1- View the first picture. 2- Name the second picture. 3- Press the button to judge whether the first picture and the second picture where the same object and color.



View task:

1- View the first picture. 2- Name the second picture. 3- Press the button to judge whether the first picture had a color gradient in it.

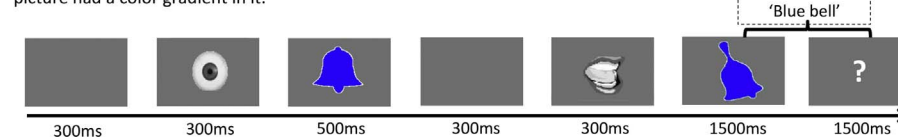


Fig. 1. Experimental design. Part A represents the three possible relations between prime and target: Shared structure and lexical items between prime and target (FullOverlap: *blue bell* – *blue bell*); shared structure but no words (Structural: *red boat*– *blue bell*); or no shared structure or noun (Lexical: *boat* – *red boat*). Part B represents the trial structure for the three possible tasks: Naming, Conceptual and View.

While several hemodynamic (Devauchelle, Oppenheim, Rizzi, Dehaene, & Pallier, 2009; Noppeney & Price, 2004; Schoot, Menenti, Hagoort, & Segaert 2014; Segaert, Kempen, Petersson, & Hagoort, 2013; Segaert, Menenti, Weber, Petersson, & Hagoort, 2012) and EEG (Boudewyn, Zirnstein, Swaab, & Traxler, 2014; Ledoux, Traxler, & Swaab, 2007; Tooley, Traxler, & Swaab, 2009) studies have looked for neural correlates of the behavioral structural priming effect, no prior study has, to our awareness, focused on the specific question of whether the simple act of combining two words can be primed. However, one of the primary regions implicated for this type of basic combination, the left anterior temporal lobe, has also figured in the hemodynamic structural priming literature, with Noppeney and Price (2004) showing a comprehension-to-comprehension priming effect in this region with ambiguous stimulus materials. This result was not, however, replicated in a subsequent comprehension study with unambiguous stimuli (Devauchelle et al., 2009), nor in the combined comprehension and production studies of Segaert et al. (2012), Segaert et al. (2013), who instead reported structural priming in the left IFG and MTG, nor Schoot et al. (2014), who found an even wider network of priming effects in the left inferior parietal cortex, left precentral gyrus, bilateral precuneus, bilateral supplementary motor cortex and the right insula. Thus overall, neuroimaging versions of the typical structural priming paradigms have mostly yielded results in regions other than where basic composition is implicated in MEG.

In sum, in contrast to the prior hemodynamic and electrophysiological work, where the objective was to look for brain correlates of the behavioral phenomenon of structural priming, our aim was to tap into more basic processes and ask whether the simple act of combining two words, an adjective and a noun, could be primed. After identifying a potentially relevant priming effect in our first study, we then conducted a second study to further test the extent to which this effect in fact reflected combinatory, as opposed to simply lexical processing.

2. Experiment 1

2.1. Method

2.1.1. Participants

Twenty-three monolingual English speakers performed the

behavioral task in Abu Dhabi (10 male, 13 female, $M = 25.72$ years, $SD = 8.33$), and 38 in San Diego (IRB procedures at UCSD precluded collecting demographic information from these subjects). All participants were right-handed, neurologically intact, had normal or corrected-to-normal vision and all provided informed written consent. Participants received a fee or course credit for their participation. MEG data were only collected in Abu Dhabi.

2.1.2. Materials and methods

On a given trial, participants performed one of three tasks, each involving the presentation of prime and target pictures. In all three tasks, the targets were always pictures of colored objects and the task on the targets was always to name them with adjective-noun combinations. The prime-task varied between Naming, View and Conceptual tasks. In the Naming task, participants named both the prime and the target pictures. In the View task, participants viewed the prime, then named the target and at the end of the trial, pressed a button only in case the prime had contained a color gradient (the gradient trials comprised 10% of the materials and were discarded in the analyses). In the Conceptual task, participants viewed the prime for the purpose of later indicating whether it matched the target, then named the target and at the end of the trial, pressed a button to indicate whether the prime and the target matched in both color and shape (Fig. 1B). Even when the prime and the target depicted the same object category, they never had the same shape, and thus the matching task invited a conceptual as opposed to a purely perceptual analysis.

The combination of different primes (object outlines or colored objects) and targets (always colored objects) resulted in three possible prime-target relations: overlapping structure with shared lexical items (FullOverlap: *blue bell/blue bell*); overlapping structure but no lexical items shared (Structural overlap: *red boat/blue bell*); and no shared structure but an overlapping lexical item (Lexical overlap: *bell/blue bell*). The 540 experimental trials were equally distributed amongst task and prime-target relation type, forming 30 trials per condition. A pictorial cue preceding stimuli presentation designated the upcoming task (Fig. 1B).

2.1.3. Procedure

Before recording, each subject's head shape was digitized using a Polhemus dual source handheld FastSCAN laser scanner (Polhemus, VT, USA). MEG data were collected in the Neuroscience of Language Lab in NYU Abu Dhabi using a whole-head 208 channel axial gradiometer system (Kanazawa Institute of Technology, Kanazawa, Japan) as subjects lay in a dimly lit, magnetically shielded room. Vocal responses were captured with an MEG compatible microphone (Shure PG 81, Shure Europe GmbH).

2.1.4. Data acquisition and preprocessing

MEG data (Blanco-Elorrieta, Ferreira, Del Prado, & Pykkänen, 2017) were recorded at 1000 Hz (200 Hz low-pass filter), noise reduced via the Continuously Adjusted Least-Squares Method (Adachi, Shimogawara, Higuchi, Haruta, & Ochiai, 2001) and epoched from 200 ms before to 700 ms after picture onset in the MEG Laboratory software (Yokogawa Electric Corporation and Eagle Technology Corporation, Tokyo, Japan). Trials containing blinks were identified by individually visualizing raw activity for each epoch. If there was any sudden, stark increase of activity, the topography for that epoch was plotted. If the magnetic field pattern had the characteristic frontal distribution of a blink, that trial was also rejected. Trials corresponding to incorrect naming, stuttering or considered outliers (oral responses quicker than 500 ms or slower than 3000 ms) were also excluded from further analysis. Additionally, trials corresponding to incorrect button presses in the Conceptual task or including gradients in the View Task were also excluded from the analyses.

A strict artifact rejection routine utilized in previous MEG production studies (Blanco-Elorrieta & Pykkänen, 2015, 2016a, 2016b, 2017; Pykkänen et al., 2014) was followed to ensure that oral artifacts were not contaminating our data. Specifically, we: (1) selected the length of the epochs such that there were more than 200 ms between the end of the epoch and the beginning of oral responses in the condition with the shortest latencies (given that motion artifacts are thought to begin roughly 200 ms before the onset of the articulation; Porcaro, Medaglia, & Krott, 2015), (2) removed any individual epochs that contained naming latencies within the length of these epochs, (3) rejected all individual epochs that contained amplitudes > 2500 fT/cm for any sensor after noise reduction, (4) visualized all individual epochs before averaging and rejected any epoch that contained sudden increases in the magnitude of the signal caused by artifacts (be it muscular movements or else), (5) applied a 40 Hz low pass filter that should eliminate any remaining oral movement from our data, given that the gamma-frequency range (> 40 Hz) is reportedly the one affected by muscle artifact contamination such as phasic contractions (Gross et al., 2013; Yuval-Greenberg & Deouell, 2009). Crucially, our design was also based on behavioral evidence supporting that conceptual and grammatical encoding for adjective-noun productions is completed before articulation begins (Alario et al., 2002; Meyer, 1996; Schriefers et al., 1999). Hence, measuring activity elicited by the production prompt, we obtained uncontaminated spatio-temporal maps of combinatorial mechanisms, such as the encoding of conceptual semantic relationships and structural syntactic relationships between elements (Ferreira & Slevc, 2007; see Pykkänen et al., 2014 for a detailed explanation of how the paradigm choice avoids motion artifact contamination). Due to the excellent noise-conditions of the MEG facility, no high pass filtering was required. The behavioral, artifact and blink rejection routines resulted in the exclusion of 17.02% of the trials (15.28% SD), leaving 447.11 trials on average per subject (82.53 SD). To estimate the distributed electrical current image in the brain at each time sample we used the Minimum Norm Approach (Hämäläinen & Ilmoniemi, 1994) as implemented in BESA Research 6.0. The sources were evenly distributed using 1500 standard locations 10% and 30% below the smoothed BESA standard brain surface (750 for each shell). Depth weighting was used in order for both deep and superficial sources to produce a similar, more focal result (as opposed to

deep sources appearing very smeared in a minimum-norm reconstruction). The spatio-temporal weighting was conducted to assign large weight to the sources that are assumed to be more likely to contribute to the recorded data. There was no constraint posited on the dipole orientation (we used free orientation), the regularization constant was 1% and we did not apply any normalization (although we did use the residual variance fit criterion; see Blanco-Elorrieta & Pykkänen, 2016a p. 13 for a full description of the Minimum Norm Estimation procedure).

2.1.5. Statistical analysis

2.1.5.1. Behavioral data. Participants' vocal responses were evaluated for each trial and trials corresponding to erroneous responses (incorrect naming, verbal disfluencies (i.e., utterance repairs, stuttering) and non-responses) were coded as errors for accuracy measures and excluded from further analysis. Additionally, oral responses quicker than 500 ms or slower than 3000 ms were considered outliers and were also excluded from further analysis. Lastly, in the Conceptual task, trials containing incorrect button presses were also coded as errors. Accuracy rates and reaction times (RTs) measured from target stimulus presentation were averaged over trials per condition and subjected to 3×3 repeated measures analyses of variance (ANOVA; main factors Task (Naming/Conceptual/View) and Prime Type (Full overlap/Structural/Lexical)). Planned contrasts were also examined with paired *t*-tests (two-tailed).

2.1.5.2. MEG data. As the main goal of the current study was to assess possible priming effects on combinatorial processes, we conducted a main analysis in the LATL (BAs 38, 20 and 21) and in the vmPFC (left and right BA11), both regions previously implicated in composition (Bemis & Pykkänen, 2011; Pykkänen et al., 2014; Westerlund & Pykkänen, 2014) although the vmPFC less consistently than the LATL (Bemis & Pykkänen, 2011; Bemis & Pykkänen, 2013; Bemis & Pykkänen, 2013; Pykkänen et al., 2014). Note that to the extent of our knowledge, no parcellation atlas contains an anatomical label encompassing uniquely the full extent of the anterior portion of the temporal lobe we targeted in these analyses. Thus, we proceeded with the Talairach Daemon (Lancaster et al., 1997; Lancaster et al., 2000) atlas utilized in previous studies (Bemis & Pykkänen, 2011; Bemis & Pykkänen, 2013; Bemis & Pykkänen, 2013; Pykkänen et al., 2014) and included all the Brodmann areas within which previous combinatorial effects have been found, while remaining cognizant of the fact that unfortunately, BA20 and 21 extend somewhat beyond the anterior part of the temporal lobe, which was the main focus of our interest. We additionally conducted a separate analysis in the left inferior frontal gyrus (LIFG; Hagoort & Indefrey, 2014) and the left angular gyrus (AG; Price, Bonner, Peelle, & Grossman, 2015), as these areas could also be sensitive to the experimental manipulation. The LIFG was included in the analyses given its importance in production research (e.g., Haller, Radue, Erb, Grodd, & Kircher, 2005; Indefrey et al., 2001; Menenti, Gierhan, Segaert, & Hagoort, 2011) and was defined as the combination of BAs 44 and 45. The AG (BA 39) was included as it has been proposed as a higher level integration area potentially involved in the combination of concepts (Binder, Desai, Graves, & Conant, 2009).

MEG activity was averaged over all sources within each Brodmann area label. For the time-course data of each label, a non-parametric cluster permutation test (Maris & Oostenveld, 2007) with 10,000 permutations was used to identify temporal clusters during which the localized activity differed significantly between conditions, corrected for multiple comparisons over time. For initial cluster selection, we adopted the parameters of prior studies: 10 adjacent time points showing an effect at an uncorrected alpha level of $p < 0.3$, (e.g., Bemis & Pykkänen, 2011; Bemis & Pykkänen, 2012; Bemis & Pykkänen, 2013; Bemis & Pykkänen, 2013; Del Prado & Pykkänen, 2014; Leiken & Pykkänen, 2014; Pykkänen et al., 2014; Westerlund & Pykkänen, 2014). Then, for each cluster surviving these thresholds, a test statistic was constructed that was equal to the summed *t* or *F*-values of the point-by-point test-statistics over the

selected cluster interval and finally, the cluster with the largest summed test statistic was chosen for further computations. Due to the last step, this test is only capable of identifying one effect within any given analysis interval and thus in order to be able to characterize potential earlier and later effects, all analyses were conducted both in an early (100–200 ms) and a mid-late (200–500 ms) time window. These time windows were determined based on the idea that priming could occur in the earliest stages of the creation of the combinatory frame as well as in later time windows, during lexical access, based on the behavioral results. Since all trials with reaction times faster than 500 ms were excluded from the analyses, we ensured these windows did not capture any late motion artifacts. For the largest cluster within an interval the corrected p -value ($p < 0.05$) was calculated as the ratio of permutations yielding a test statistic greater than the actual observed test statistic. To protect our analysis against false positives across multiple labels within the same analysis (L ATL and vmPFC or AG and LIFG) a false discovery rate (FDR; Benjamini & Hochberg, 1995; Genovese, Lazar, & Nichols, 2002) of 0.05 was used.

2.2. Results

2.2.1. Behavioral results (San Diego)

Mean naming latencies and accuracies for San Diego participants are plotted in Fig. 2A. We submitted naming latencies measured from target stimulus presentation to a 3×3 ANOVA with the factors Prime Task (Naming/Conceptual/View) and Prime Type (FullOverlap/Structural/Lexical), which revealed that RTs varied as a function of the Prime Type ($[F(2,74) = 146.5; p < 0.0001]$) and the performed task ($[F(2,74) = 19.99; p < 0.0001]$). Additionally, we also observed a reliable interaction between Prime Task and Prime Type ($[F(4,148) = 5.38; p < 0.0001]$). We unpacked this interaction by looking into Prime Type effects within each task with 1×3 ANOVAs, which showed that in all tasks, the relation between the prime and the target influenced the naming latencies (Naming $[F(2,74) = 101.9; p < 0.0001]$; Conceptual $[F(2,74) = 56.85; p < 0.0001]$ and View $[F(2,74) = 31.75; p < 0.0001]$). Planned two-tailed t -tests showed that in all tasks, participants were the quickest when there was full overlap between prime and target phrases (in Naming $[t(37) = 9.59; p < 0.0001]$; Conceptual $[t(37) = 6.62; p < 0.0001]$ and View $[t(37) = 5.28; p < 0.0001]$). Additionally, the t -tests showed that participants were quicker when the conditions overlapped only lexically than only

structurally (in Naming $[t(37) = 5.28; p = 0.01]$, Conceptual $[t(37) = 3.81; p = 0.0004]$ and View $[t(37) = 2.82; p = 0.007]$). Thus this pattern tracked the number of shared lexical items quite closely (Fig. 2A, left panel).

Accuracy data were submitted to the same 3×3 ANOVA with main factors Prime Task (Naming/Conceptual/View) and Prime-Type (FullOverlap/Structural/Lexical). This analysis, however, only revealed a main effect of Prime Type $[F(2,74) = 6.41; p = 0.002]$. 1×3 ANOVAs conducted within each of the tasks revealed that this effect was driven by the difference between prime types in Naming $[F(2,74) = 7.35; p = 0.001]$, with participants being significantly more error prone when the prime and the target overlapped structurally. This effect was not observed in either the Conceptual $[F(2,74) = 1.77; p = 0.17]$ or in the View tasks $[F(2,74) = 1.43; p = 0.24]$ (Fig. 2A, right panel).

2.2.2. Behavioral data of MEG recordings

Behavioral data (naming latencies and accuracies) collected during MEG recordings were submitted to the same analyses as the data collected in San Diego. 3×3 ANOVAs (factors: Prime Task (Naming/Conceptual/View) and Prime Type (FullOverlap/Structural/Lexical) performed on naming latencies showed that both the task $[F(2,50) = 24.2; p < 0.0001]$ and the prime type $[F(2,50) = 83.85; p < 0.0001]$, significantly influenced reaction times. We further characterized Prime Type effects within each task with 1×3 ANOVAs, which showed that in all tasks, naming latencies varied as a factor of the priming type (Naming $[F(2, 50) = 19.35; p < 0.0001]$; Conceptual $[F(2,50) = 49.0; p < 0.0001]$ and View $[F(2,50) = 23.16; p < 0.0001]$, Fig. 2B). Mirroring the results obtained in San Diego, planned two-tailed t -tests showed that in all tasks, participants were quicker to name the targets that fully overlapped with the prime than the targets that only overlapped lexically (in Naming $[t(25) = 3.41, p = 0.002]$, Conceptual $[t(25) = 6.45; p < 0.0001]$ and View $[t(25) = 4.22; p < 0.0001]$). However, they were quicker naming targets that overlapped lexically than structurally (Naming $[t(25) = 2.73; p = 0.01]$, Conceptual $[t(25) = 3.9; p = 0.0006]$ and View $[t(25) = 2.2; p = 0.03]$). A small numerical speed-up was observed for Structural targets as compared to their primes (11 ms), suggesting a purely structurally driven trend. However, this difference did not approach significance ($p = 0.52$).

The results of the 3×3 ANOVA on error rate revealed a main effect of Prime Task $[F(2,50) = 16.44; p < 0.0001]$, a main effect of Prime

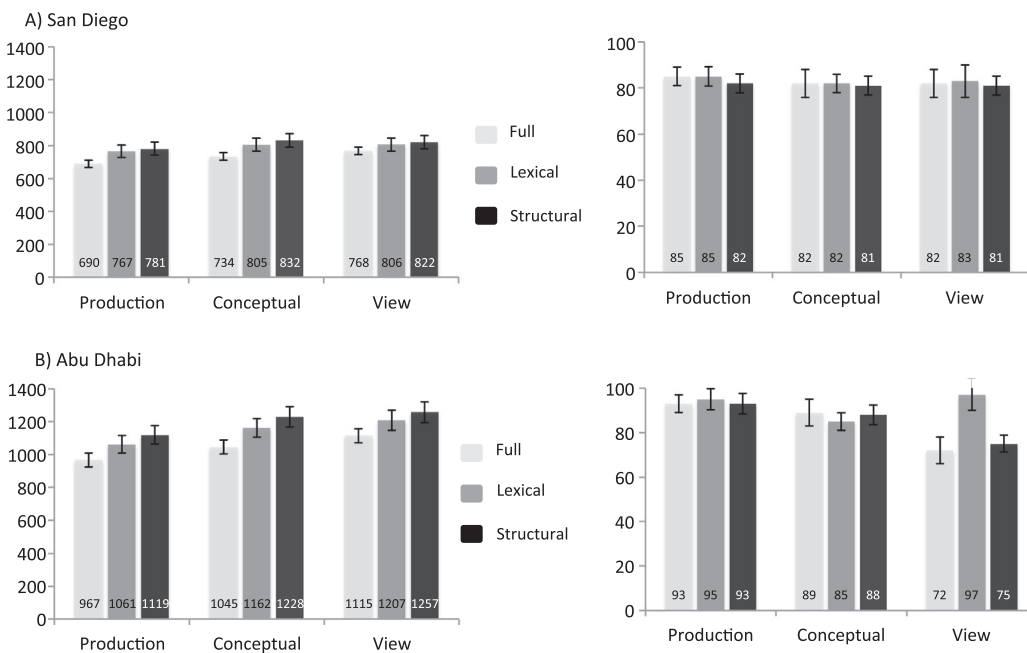


Fig. 2. Mean reaction times as a function of the performed Prime Task and the visualized Prime Type. Naming latencies were measured from target stimulus presentation. Numbers at the bottom of the bars display means for each condition. Error bars show SEM. In both A) and B), left panels correspond to Reaction time data and right panels show accuracy.

Type [$F(2,50) = 12.35$; $p < 0.0001$] and a reliable interaction between Prime Task and Prime Type [$F(4,100) = 13.63$; $p < 0.0001$]. 1×3 ANOVAs within each task revealed that these effects were caused by Prime Type differences in the View task [$F(2,50) = 74.72$; $p < 0.0001$], but not in the Naming [$F(2,50) = 0.346$; $p = 0.7$] or Conceptual tasks [$F(2,50) = 0.259$; $p = 0.7$] (Fig. 2B, right panel).

2.2.3. MEG results

One of the main innovations of the current study was that both prime and target productions were analyzed and in fact, priming effects were assessed based on the relation between the activities in the two. Specifically, in order to evaluate whether the activities in the target elements were primed, we had to first find combinatory effects in the prime: If no combinatory activity was observed in the prime, we would not be able to assess whether these combinatory activities were primed in the target. Based on our previous studies (Bemis & Pykkänen, 2011; Bemis & Pykkänen, 2013; Bemis & Pykkänen, 2013; Pykkänen et al., 2014; Westerlund & Pykkänen, 2014) we expected these combinatory effects in the prime to manifest by showing increased activity for combinatory as compared to non-combinatory conditions.

Thus, the first analysis aimed to identify combinatory effects during prime production to establish whether our premise was met. We conducted a one-way ANOVA (Prime Type: FullOverlap/Structural/Lexical) within Naming, focusing on regions previously implicated in composition (LATL and vmPFC). The results (plotted in Fig. 3) showed a main effect of Prime Type in Brodmann areas overlapping with the LATL (BA38 [100–158 ms; $p = 0.004$] and BA20 [100–127 ms; $p = 0.006$]) and the vmPFC (130–167 ms; $p = 0.01$), as well as a marginally reliable effect in BA21 [110–131 ms; $p = 0.09$]. As expected, these effects were driven by both combinatory conditions (FullOverlap and Structural) eliciting reliably greater activity than the non-combinatorial (Lexical) condition. Specifically, two-tailed t -tests showed that FullOverlap elicited more activity than Lexical overlap in BA38 (100–169 ms; $p = 0.01$), BA20 (100–156 ms; $p = 0.01$) and BA21 (100–168 ms; $p = 0.05$), as well as in the vmPFC (100–168 ms; $p = 0.01$). The condition with Structural overlap also elicited reliably more activity than the non-combinatorial Lexical overlap condition in BA38 (100–173 ms; $p = 0.01$) and the vmPFC (100–207 ms; $p = 0.01$) (Fig. 3).

Subsequently, we examined whether these combinatory effects could be primed. We ran the same one-way ANOVA (Prime Type: FullOverlap/Structural/Lexical) on target data and the results revealed a reliable effect of Prime Type in BA38 (114–147 ms; $p = 0.04$) (Fig. 3). Contrary to the purely combinatory effects observed during prime processing, where both combinatory conditions (Structural and FullOverlap) elicited greater activity than the non-combinatorial condition (Lexical), the effect during target processing was caused by FullOverlap condition eliciting reliably more activity than both Structural and Lexical. This pattern was clearly observed on the cluster means; however, these effects did not reach reliability in the pairwise comparisons.

Neither in the Conceptual (Additional Fig. 1) nor in the View (Additional Fig. 2) tasks did we observe combinatory activity in the primes (all clusters $p > 0.1$), which precluded us from investigating priming effects on targets in these tasks. We also did not identify any effect in the other analyzed regions in any of the tasks (LIFG and AG; all clusters $p > 0.1$).

2.3. Discussion

In Experiment 1, we tested whether the composition-related MEG activities elicited by the construction of a simple adjective-noun combination could be primed. During the main experimental task, participants named target pictures of colored objects with adjective-noun combinations (*red boat*) after having named fully overlapping primes (*red boat*), only structurally overlapping primes (*blue bell*), or only lexically overlapping primes (*boat*). During prime naming, combinatory

productions elicited more localized activity than one-word productions in areas of left anterior temporal and ventromedial prefrontal cortex, replicating results from a prior study with the same contrast (Pykkänen et al., 2014). These effects were not obtained in the View or Conceptual tasks, suggesting that they reflected combinatorial processes of language production, as opposed to non-linguistic binding of visual or conceptual features. The lack of vmPFC engagement on the conceptual primes is in contrast to the findings of Bemis and Pykkänen (2013), who did observe a vmPFC increase for semantically complex pictures in a similar task. Given the mixed results, no strong conclusion should yet be drawn from the absence of medial prefrontal effects in the Conceptual task.

The elicitation of these frontotemporal combinatory effects during prime naming fulfilled the prerequisite for the main goal of our study, which was to test whether these effects could subsequently be primed during target naming, which always involved the production of adjective-noun combinations. This analysis was only performed for the Naming task on primes, since the View and Conceptual tasks did not show combinatory effects on the prime. An effect of Prime Type relation was indeed observed in the activity reflecting the planning stages of the target productions in the Naming task, though it was limited to activity localized in BA38, i.e., the temporal pole. This was in contrast to the extent of the combinatory effects during prime production, which covered all areas overlapping with middle and ventral left anterior temporal cortex and the vmPFC (i.e., BA38, BA20, BA21, BA11). Thus, unsurprisingly, the effect of priming on the combinatory activity of targets, which were uniformly combinatory, was subtler than the effect of the presence vs. absence of composition on primes (i.e., the contrast of saying one word vs. a phrase). The spatial contrast between the composition effect on the primes and the more confined priming effect on the targets suggests that only some of the regions participating in composition encode primeable memory representations. Most importantly, the effect of Prime Type on target productions was almost identically timed with the effect of composition on prime productions, suggesting that the same computation was reflected in the combinatory effect during primes and the priming effect during targets. Spatially, our priming result also matched the localization of structural priming in Noppeney and Price (2004).

However, a crucial aspect of our priming effect was that it only obtained for the fully overlapping pairs and thus was not a pure reflection of shared structure. Many hypotheses are capable of explaining this finding. The fact that priming was only observed in the presence of two shared lexical items of course makes it possible that the effect could have been purely lexical in nature, though its absence for the single word repetition in the *boat – red boat* pairs would be somewhat puzzling under this account. Nevertheless, a purely lexical account cannot yet be ruled out. More interestingly for the present purposes, the priming could reflect early combinatory planning that is facilitated in the presence of conceptual overlap. Such facilitation could require either full conceptual overlap or partial overlap, and in the latter case, the effect could be driven either by the noun or the adjective. If the effect was driven by a shared noun, i.e., the head of the phrase, this would pattern with prior behavioral literature on structural priming, which is at least sometimes “boosted” if the syntactic head of the prime and target expressions is lexically identical (Pickering & Branigan, 1998; Tooley et al., 2009; Traxler, 2015). In contrast, if the effect depended on the shared adjective, this would align with a behavioral literature on relational priming within conceptual combinations. Specifically, there is evidence that the relation that links the two concepts of noun-noun combinations can be primed only if the modifier is shared (Gagné, 2001; Gagné, 2002; Gagné & Shoben, 2002; Gagné, Spalding, & Ji, 2005). For example, under this account, the MADE-OF relation of material-object combinations is predicted to be primed when the modifier (i.e., the material) is shared, as in *wood table – wood floor*, but not when the object is shared, as in *wood table – metal table*. Our second experiment was designed to distinguish between all these possibilities.

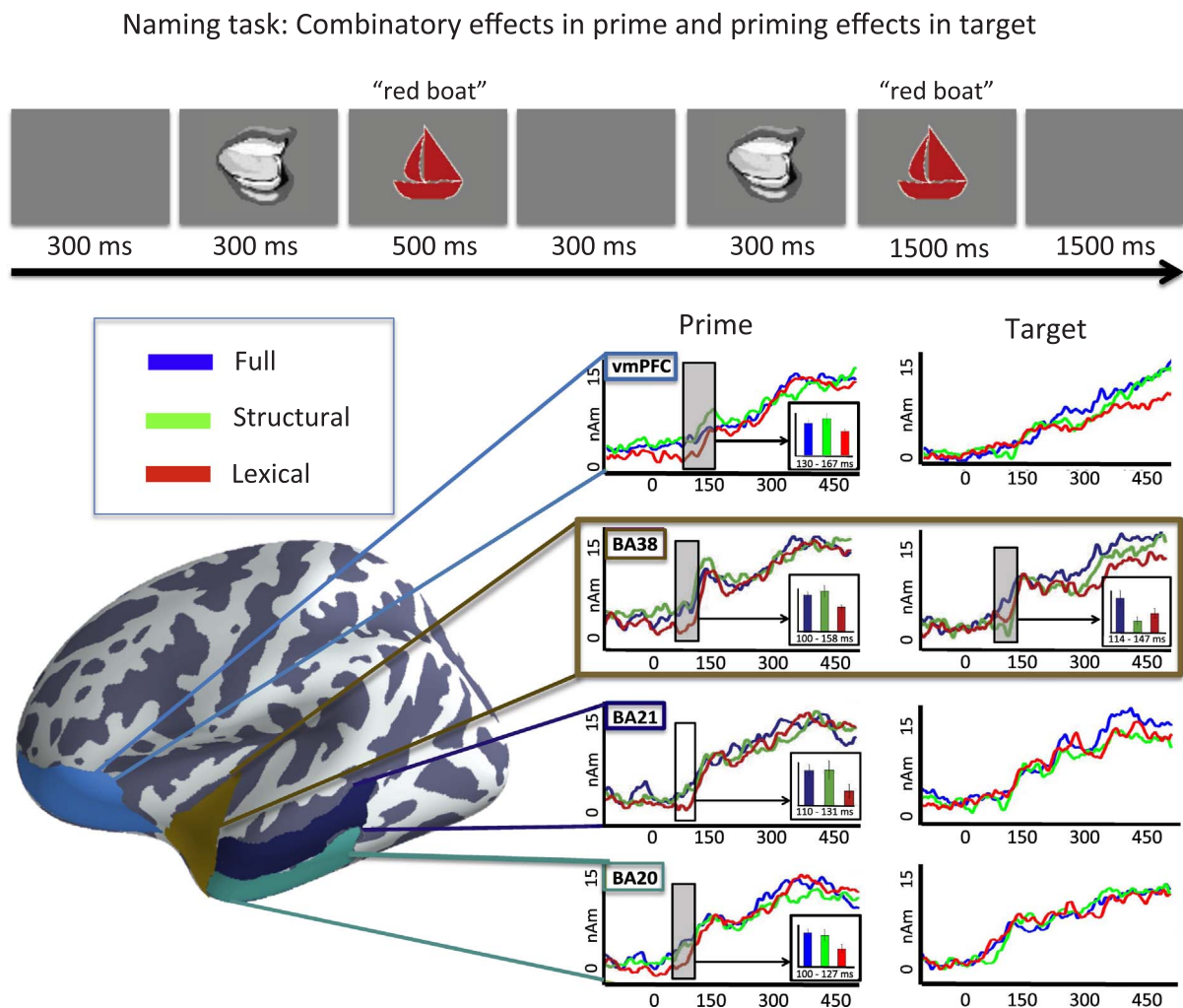


Fig. 3. ROI results for one-way ANOVAs (Prime Type: FullOverlap, Structural, Lexical) for the Naming task, activation averaged across subjects. A freeSurfer average brain illustrates the spatial distribution of the BAs included in the analyses, color-coded by Brodmann area. On the waveform plots, the shaded regions indicate that the difference in activity between the tested conditions was significant at a $p = 0.05$ value (corrected), the boxed regions indicate marginally reliable results ($p < 0.1$). Significance was determined using a non-parametric permutation test (Maris & Oostenveld, 2007) performed from 100 to 200 and 200 to 500 ms (10,000 permutations). The means of all conditions during the length of the clusters are displayed in a bar plot within each waveform plot. Additionally, under the title, the trial structure for the Naming task is displayed.

One perhaps important aspect of the priming effect in Experiment 1 was that instead of a decrease in brain activity, priming surfaced as an increase of BA38 amplitude. While activity decreases (repetition suppression effects) are more intuitive and better understood as reflections of repetition or primed processing, in the broader context of brain correlates of repetition effects, repetition enhancements, i.e., activity increases as a result of repetition, are not uncommon, as reviewed by Segaert et al. (2013) and reported in multiple prior language studies (Copland, de Zubicaray, McMahon, & Eastburn, 2007; Kotz, Cappa, von Cramon, & Friederici, 2002; Rossell, Price, & Nobre, 2003; Weber, Lau, Stillerman, & Kuperberg, 2016; Wible et al., 2006). Further, repetition effects can also shift from initial repetition enhancement to repetition suppression within a few hundred milliseconds (Marinkovic et al., 2003), showing that the brain correlates of repetition can be quite complex. Converging evidence has been found for non-linguistic visual stimuli in a number of paradigms in which repetition has elicited increased occipital activation (e.g., Bar et al., 2001; Ress & Heeger, 2003) and a memory literature in which repetition enhancement has been linked to repetition of stimuli that are explicitly task-relevant to the participant (Brown & Aggleton, 2001). Although repetition enhancements are reported less commonly than repetition suppressions, their existence is not surprising in light of theoretical models of the computational anatomy of repetition (for a review, see, Gotts,

Chow, & Martin, 2012). In particular, in the so-called synchrony model, repetition of stimuli leads to more synchronous neural firing and consequently more efficient processing (Gilbert, Gotts, Carver, & Martin, 2010; Gotts, 2003). As support for this model, results remarkably similar to ours have been reported in MEG measurements of covert picture naming: amplitudes of evoked responses were increased for repeated pictures in ventral temporal and occipital cortical areas as well as in prefrontal cortex (Gilbert et al., 2010). These increases were all observed early, at 100–200 ms after stimulus onset, consistent with the timing of our effects. Thus the activity increases we observed as a function of repetition may reflect this type of improved temporal coordination, resulting in higher amplitudes in stimulus locked early responses.

It should also be noted that the relation between repetition effects in brain measurements vs. subsequent behavioral priming is far from established: repetition enhancement can lead to behavioral facilitation effects (Segaert et al., 2013 for a review), inhibitory effects (Egner & Hirsch, 2005) or no accompanying behavioral effects (Gagnepain et al., 2008; Kouider, De Gardelle, Dehaene, Dupoux, & Pallier, 2010; Turk-Browne, Yi, Leber, & Chun, 2007). In this study we observed that the MEG results are not directly predictive of the behavioral effects, given that our behavioral results were consistent with lexical priming but MEG results were more consistent with a lexically boosted structural priming pattern (given the

absence of priming for *boat – red boat*). This difference can perhaps be due to the fact that our MEG effects plausibly reflected the earliest stages of the composition of the combinatorial message whereas the behavioral measures most directly reflect effects occurring later in the time course. In other words, the MEG signal may reflect an early facilitation effect on building the same representational frame while behavioral responses may instead reflect facilitation effects on repeatedly retrieving identical items to fit in that frame, which would by hypothesis occur later in the time course.

3. Experiment 2

Experiment 2 was designed to address (i) whether the priming effect observed in Experiment 1 was in fact dependent on composition as opposed to the mere repetition of the same two lexical items in primes and targets; and (ii) if it was dependent on composition, to establish how much and what type of lexical-conceptual overlap would be required for its elicitation. Even if the effect required full conceptual identity, it could still be composition related in that it could reflect priming of the same combinatorial conceptual representation. In this case, the effect should be elicited for phrase repetition (*red boat – red boat*) but not for single word repetition (*boat – boat*). The first aim of Experiment 2 was to distinguish between these two possibilities with a simple design where lexical identity (Same vs. Different) was crossed with Composition (Combinatory vs. Non-combinatory). This yielded the following four prime-target pairs: *red boat – red boat*, *blue bell – red boat*, *boat – boat*, *bell – boat*, (Fig. 4A). Since the relevant BA38 priming effect was only observed in the production-to-production task of Experiment 1, only this task was employed in Experiment 2.

Should the early priming effect be limited to combinatorial productions, we then planned to test how much lexical overlap was required for its elicitation. To achieve this, we included prime-target pairs with only a shared noun (*black boat – red boat*) and only a shared adjective (*red cup – red boat*). The former exemplified the situation, discussed above, in which lexically boosted structural priming is commonly observed (e.g., Pickering & Branigan, 1998) and the latter the situation in which relational priming has been reported in conceptual combinations. These two conditions were compared to the two combinatorial conditions of the first part of Experiment 2 (combinatorial phrases with full vs. no lexical overlap), thus covering the whole spectrum of possible lexical overlap in adjective-noun phrases. This resulted in an additional 2×2 design, crossing Adjective Repetition (Same vs. Different) with Noun Repetition (Same vs. Different; see Fig. 4B). Please note that since two conditions were common to the two 2×2 designs (fully lexically overlapping combinatorial and non lexically-overlapping combinatorial conditions), both 2×2 designs were evaluated in a single experiment with 6 conditions.

3.1. Method

Methods for this experiment were maximally parallel to Experiment 1 and thus only the methods that differed from Experiment 1 will be explained below.

3.1.1. Participants

Twenty monolingual English speakers participated in this experiment conducted in Abu Dhabi (11 male, 9 female, $M = 28.76$ years, $SD = 9.55$). All participants were right-handed, neurologically intact, had normal or corrected-to-normal vision and all provided informed documented consent. Participants received a fee for their participation. Due to problems during the head-scanning stage, 3 participants were excluded from further analysis.

3.1.2. Materials and methods

Participants were presented with a picture on a gray background and they were asked to name it aloud. If the picture was an outline of an object, participants were asked to name only the shape of the picture. If

the picture was a colored object, participants had to name both the color and the shape of the picture. As in Experiment 1, all trials contained a prime and a target element, and the relation between the two defined experimental conditions. Specifically, there were six possible prime-target relations. Four of them were combinatorial conditions of adjective-nouns; namely, same adjective – same noun in prime and target (Full Overlap: *red boat/red boat*); same adjective – different noun (Same Adjective_Different Noun: *red cup/red boat*); different adjective – same noun (Different Adjective_Same Noun: *black boat/red boat*) and different adjective – different noun in prime and target (No Overlap: *blue bell/red boat*). The other two conditions were non-combinatorial conditions and contained specifically same noun in prime and target (Full overlap: *boat/boat*) and different noun in prime and target (No Overlap: *bell/boat*) (for trial design and examples of all experimental conditions see Fig. 4C). Experimental stimuli were combinations of 18 different objects (bag, bell, boat, bow, cane, cross, cup, glass, hand, heart, house, lamp, leaf, lock, note, plane, tree and star) and 6 different colors (black, blue, green, pink, red and white). All items were monomorphemic and monosyllabic to avoid effects such as delayed naming latencies and greater motor preparation for words with more syllables. Additionally, we used the English Lexicon Project (Balota et al., 2007) to match as optimally as possible all stimuli words on lexical-level variables. The object nouns were slightly shorter than the color words on average (4.11 vs. 4.4 characters) but this difference was not significant [$t(21) = -0.79$; $p = 0.29$]. Additionally, the two word classes did not differ significantly in terms of mean reaction time either (M object nouns = 580 ms; M color words = 590 ms; [$t(21) = -0.48$; $p = 6.33$]).

Each color was presented 24 times and each object 12 times, 8 times combined with a color and 4 times as an outline. Half of the occurrences of each item were as the prime and half as the target element in the trial. Each object only appeared once as a prime and once as a target in each experimental block and there were at least 7 full trials (14 stimuli) between a given object appearing as a prime and as a target within a block. We created 6 experimental lists, each consisting of 216 trials (36 trials per condition), and each participant was assigned two of these lists (1 & 2, 3 & 4 or 5 & 6). Stimuli were kept constant across all conditions, thus assuring that there was no perceptual variation amongst them.

3.1.3. Procedure

The behavioral, artifact and blink rejection routines were conducted as in the Naming task of Experiment 1. This resulted in the exclusion of more than 85% of the trials for two participants, who were excluded from further analysis. For the remaining participants, 24.4% of the trials were rejected on average (12.69% SD), leaving 326.51 trials on average per subject (54.73 SD).

3.1.4. Statistical analysis

3.1.4.1. Behavioral data. Behavioral data were analyzed mirroring the two 2×2 ANOVAs that were applied to the MEG data. Specifically, we conducted a 2×2 ANOVA on target reaction time data with main factors Lexical Identity (Same/Different) and Composition (Combinatory/Non-combinatory), and another with Adjective Repetition (Same/Different) and Noun Repetition (Same/Different) as main factors.

Additionally, accuracy rates were averaged over trials per condition and subjected to 2×6 repeated measures analyses of variance (ANOVA; main factors Position (Prime/Target) and Prime Type (Combinatory: Full Overlap/Same Adj_Different Noun/Different Adjective_Same Noun/No Overlap and Non-Combinatory: Full Overlap/No Overlap).

3.1.4.2. MEG data. This experiment aimed to further our understanding of the priming effects observed in the Naming task of Experiment 1. Hence, we focused our analyses of the MEG data (Blanco-

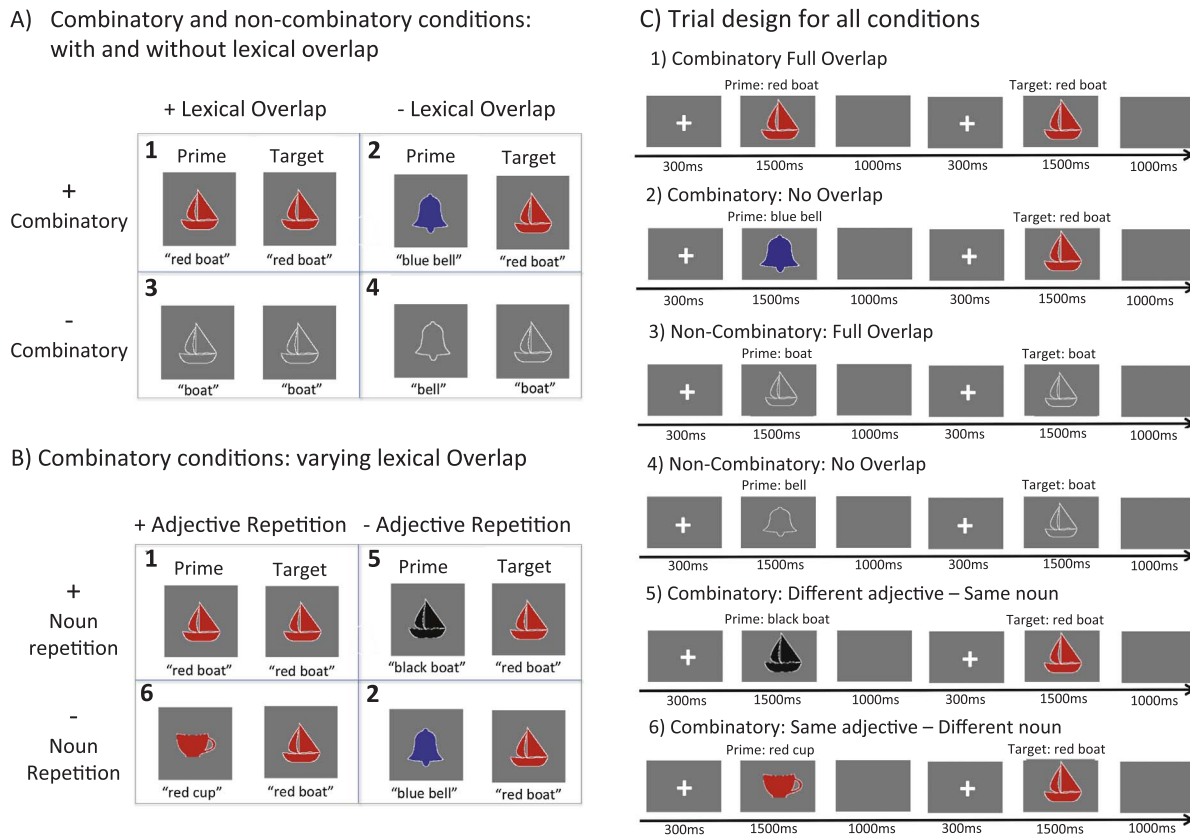


Fig. 4. Design of Experiment 2. In all conditions participants were asked to name the object presented on the screen using (i) a color-object combination (*blue bell*) when the picture was a colored object and (ii) a noun (*boat*) when the picture was an outline. In all cases, the relation between prime and target determined experimental conditions. Panel A shows the 2 × 2 design crossing lexical overlap (Same vs. Different) and Composition (Combinatory vs. Non-combinatory). Panel B shows the 2 × 2 design crossing Noun Repetition (Same vs. Different) and Adjective Repetition (Same vs. Different). Panel C shows the trial structure for each of the 6 conditions of Experiment 2.

Elorrieta et al., 2017) on the area where this effect was observed, i.e., the LATL. However, BA21 was excluded from this analysis given that the combinatorial effect in the prime in Experiment 1 was not reliable (i.e., the premise to investigate priming on targets was not met). Thus, the analyses in Experiment 2 exclusively included BA 38 and 20.

The first goal of this experiment was to address whether the priming effects observed in targets of Experiment 1 reflected composition of the same combined concept or simply processing of the same concept (complex or not). For this, we first conducted a 2 × 2 ANOVA with the main factors Lexical Identity (Same/Different) and Composition (Combinatory/Non-combinatory) in the same time window where the priming effect was observed in Experiment 1 (100–200 ms). Our main question was whether the priming effect of Experiment 1 was specifically elicited for combinatory and not for non-combinatory stimuli, and to address this, we employed the same statistical test as used in prior research aimed at revealing combinatory effects in two-word phrases that are absent for two word lists (Bemis & Pykkänen, 2011). Specifically, while the cluster level statistics of the main effects are calculated using the F-values from the repeated measures ANOVA, for the cluster level statistics of the interaction, a paired t-test was performed at each time point of the analyzed window between conditions that varied in Lexical Identity (Same/Different) within each Composition level (Combinatory vs. Non-combinatory respectively). This produced two t-values for every time point in the cluster: one corresponding to the difference in activity between the two combinatorial conditions (with and without lexical overlap) and one corresponding to the difference in activity between the two Non-Combinatory single word conditions (with and without lexical overlap). The absolute value of the second t-value was then subtracted from the first, yielding a component test statistic which was then used in the permutation tests

(Bemis & Pykkänen, 2011; Blanco-Elorrieta & Pykkänen, 2016b). Data for both main effects and the interaction were then subjected to 10,000 random permutations and the final corrected p-value (alpha: p < 0.05) of the observed data was calculated as the ratio of permutations yielding a test statistic greater than the actual observed test statistic. We used an FDR of 0.05 to correct for multiple comparisons across the two analyzed areas.

The second goal of this experiment was to investigate the extent to which the effect observed in the first part of Experiment 2 might be observed even with phrasal primes with partial lexical overlap. Therefore we ran a 2 × 2 ANOVA within phrase conditions with main factors Adjective Repetition (Same/Different) and Noun Repetition (Same/Different). Please note that two conditions were common to these two designs (fully lexically overlapping combinatory and non lexically-overlapping combinatory), which allowed us to evaluate both 2 × 2 designs in a single experiment with 6 conditions.

Since the goal of this analysis was to explore further the effect observed in the first part of Experiment 2, this analysis was only run in the time window where such effect was observed. Please note that even though cluster permutation tests are mostly used when testing long time-windows (as this test protects against multiple comparisons over time), there is no drawback for applying them in shorter time windows. Thus, in order to parallel the methods of all our previous analyses, we used the same analysis type in a smaller time window, which although less frequent does not pose any statistical concern. Additionally, as we did not hold any particular hypotheses regarding the direction of possible interactions, F values from the repeated measures ANOVA were calculated for each time point within the analyzed time windows and were used in the permutation tests to calculate the cluster level statistic of the main effects as well as the interactions.

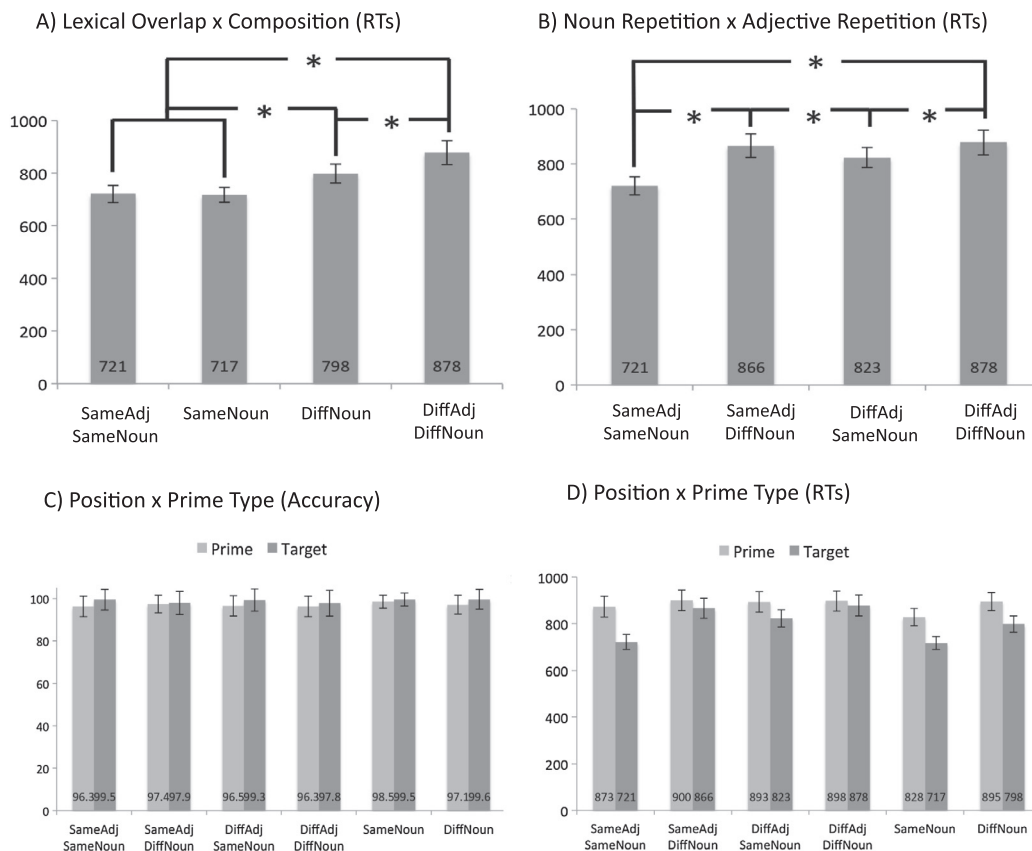


Fig. 5. Behavioral data of Experiment 2. Panel A shows reaction time averages per condition for a 2 × 2 the ANOVA crossing Lexical Overlap (Same/Different) and Composition (Phrase/Single Word. Panel B shows the reaction time averages per condition for the 2 × 2 design crossing Noun Repetition (Same vs. Different) and Adjective Repetition (Same vs. Different). Panel C and D show 2 × 6 ANOVAs including all experimental conditions crossing main factors Position: Prime/Target and Prime Type: SameAdj_SameNoun/SameAdj_DiffNoun/DiffAdj_SameNoun/DiffAdj_DiffNoun/SameNoun/SameAdj) on accuracy data and reaction times respectively. In all cases numbers at the bottom of the bars display the means for each condition and error bars show SEM. In panels A, B and D the Y axis represents milliseconds, in panel C the Y axis represents the percentage of accuracy. In parts A and B significant pairwise differences between conditions are marked by an asterisk sign.

3.2. Results

3.2.1. Behavioral results

To obtain a full characterization of possible behavioral structural priming effects, we performed the same 2 × 2 ANOVAs on target RTs as on MEG data (Fig. 5). The ANOVA including Lexical Identity (Same/Different) and Composition (Combinatory/Non-combinatory) as main factors revealed a main effect of Composition [$F(1,14) = 7.32$; $p = 0.01$], a main effect of Lexical Identity [$F(1,14) = 134.1$; $p < 0.0001$] and a reliable interaction between the two [$F(1,14) = 46.14$; $p < 0.0001$] (Fig. 5A). Planned *t*-tests showed that conditions including repetition of elements were significantly faster than conditions with no overlap (Full Overlap vs. No Overlap within combinatory conditions [$t(14) = 12.98$; $p < 0.0001$] and Full Overlap vs. No Overlap in non-combinatory conditions [$t(14) = 7.04$; $p < 0.0001$]). Additionally, we found that the two conditions including lexical overlap did not differ from each other (fully overlapping Combinatory vs. Non-Combinatory conditions [$t(14) = 0.29$; $p = 0.77$]), but the Combinatory condition with no lexical overlap was significantly slower than Non-Combinatory condition with no lexical overlap [$t(14) = 3.98$; $p = 0.001$].

The 2 × 2 analysis within combinatory conditions including main factors Noun Repetition (Same/Different) and Adjective Repetition (Same/Different), aimed at investigating the effect of lexical overlap in structural priming, revealed a main effect of Adjective Repetition [$F(1,14) = 86.85$; $p < 0.0001$], a main effect of Noun Repetition [$F(1,14) = 104.2$; $p < 0.0001$] and a reliable interaction between the two [$F(1,14) = 103.8$; $p < 0.0001$] (Fig. 5B). Planned *t*-tests showed that conditions including repetition of a noun were faster than those including repetition of an adjective. Specifically, Full Overlap was faster than Same Adjective_Different Noun [$t(14) = 14.89$; $p < 0.0001$] and No Overlap [$t(14) = 12.98$; $p < 0.0001$], and Different Adjective_Same Noun was quicker than both Same Adjective_Different Noun [$t(14) = 4.08$; $p = 0.001$] and No Overlap [$t(14) = 4.97$;

$p = 0.0002$]. Thus, the priming in this analysis seems to have been driven by noun repetition.

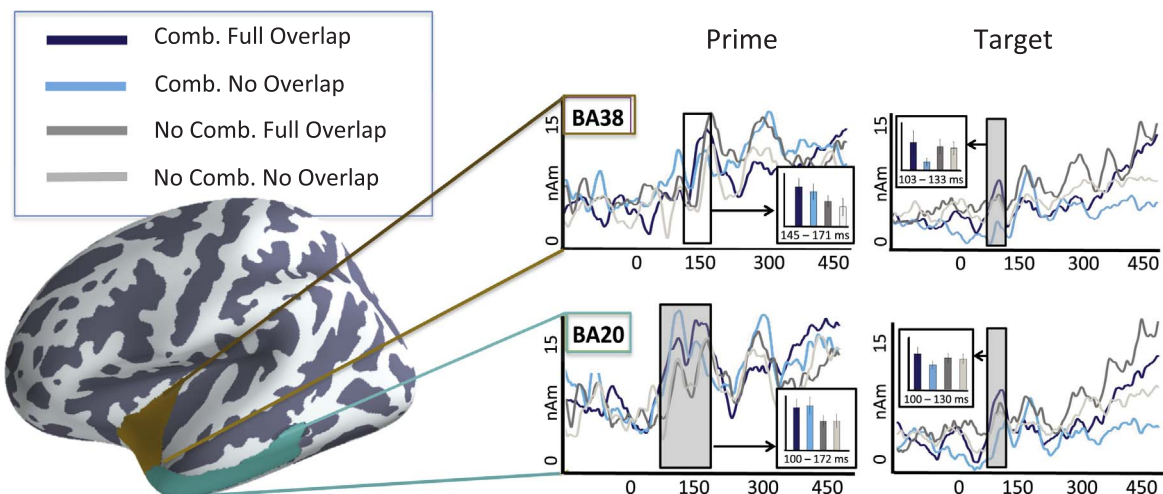
Lastly, although accuracy was almost at ceiling, we analyzed whether participants were more accurate on target than prime trials. We conducted a 2 × 6 ANOVA (main factors Position: Prime/Target and Prime Type: Same Adjective_Same Noun/Same Adjective_Different Noun/Different Adjective_Same Noun/Different Adjective_Different Noun/Same Noun/Same Adjective) on accuracy data. This analysis revealed a reliable main effect of Position [$F(1,14) = 24$; $p = 0.0002$], showing that participants were in fact, significantly more error prone on prime than target elements (Fig. 5C). In order to establish whether this effect was a speed-accuracy trade off we conducted a post-hoc 2 × 6 ANOVA on RTs and found that in fact, prime items were reliably slower than target items [$F(1,14) = 146$, $p < 0.0001$] (Fig. 5D).

3.2.2. MEG results

The 2 × 2 ANOVA with main factors Lexical Identity (Same/Different) and Composition (Combinatory/Non-combinatory) revealed a reliable main effect of Composition in the primes in BA20 [100–172 ms; $p = 0.01$] and a similar weaker effect in BA38 [145–171 ms; $p = 0.06$] (Fig. 6A). In the targets, the analysis in the same time window revealed a reliable interaction between Lexical Identity and Composition in BA38 [103–133 ms; $p = 0.03$] and BA20 [100–130 ms; $p = 0.02$], caused by increases of overlapping over non-overlapping phrases (two-tailed *t*-tests: BA20 [100–131 ms; $p = 0.06$]) and no difference between overlapping and non-overlapping single words.

We subsequently expanded this analysis to establish the extent to which the observed priming effect was contingent upon full lexical overlap between primes and targets. For this purpose, we conducted a 2 × 2 ANOVA on composed conditions with varying degrees of lexical overlap between primes and targets. Since this analysis directly followed the previous one, it was conducted in the time window where the previous priming effects were observed (100–150 ms). Main factors for

A) Comparison of combinatory and non-combinatory conditions, with and without lexical overlap



B) Comparison of combinatory conditions, with varying degrees of lexical overlap

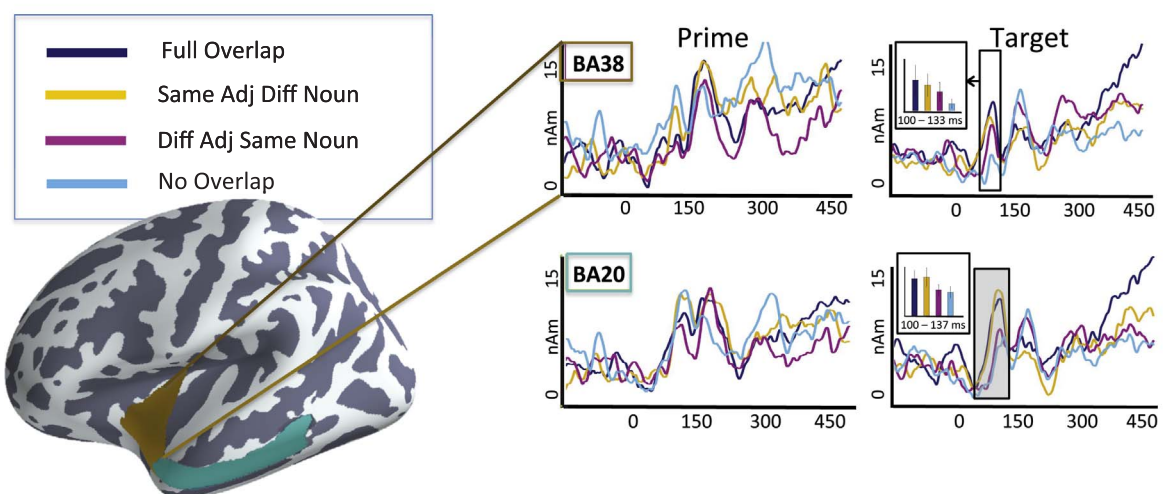


Fig. 6. ROI results of Experiment 2, activation averaged across subjects. Within each section, a freeSurfer average brain illustrates the spatial distribution of the BAs included in the analyses, color-coded by Brodmann area. On the waveform plots, the shaded regions indicate that the difference in activity between the tested conditions was significant at a $p = 0.05$ value (corrected). The boxed regions indicate marginally reliable results ($p < 0.1$). Significance was determined using a non-parametric permutation test (Maris & Oostenveld, 2007) performed from 100 to 200 in part A and 100 to 150 ms in part B (10,000 permutations). The means of all conditions during the length of the clusters are displayed in a bar plot within each waveform plot.

this analysis were Noun Repetition (Same/Different) and Adjective Repetition (Same/Different). As expected, given that all conditions were combinatorial, this analysis revealed no differences in prime elements. However, in target elements, we observed a reliable main effect of Adjective Repetition in BA20 [100–137 ms; $p = 0.01$] and a similar but marginal effect in BA38 [100–133 ms; $p = 0.06$], suggesting that structural priming effects were driven by adjective overlap (Fig. 6B). The spatial center of the priming effect was slightly different in Exp. 2 than in Exp. 1, given that in Exp. 1 only BA 38 was reliable, but this type of difference should be taken with caution given the somewhat limited spatial resolution of MEG.

Since now across both experiments, our priming pattern followed the generalization that every time the prime and target pictures shared a color, priming was observed, we went back to Experiment 1 data to analyze the target responses in the View and Conceptual tasks, which previously were not analyzed since their primes did not show combinatorial effects. If the priming was due to perceptual color priming, the View and Conceptual tasks should show the priming effect, whereas if it was driven by adjective-led composition, this should not be the case. To test this, we ran 1×3 ANOVAs (Prime Type: Full Overlap/Structural/

Lexical) in the same time-window (100–200 ms) and areas (BA20 and 38) where the priming effects had been localized for the Naming tasks in Experiments 1 and 2. These analyses did not identify any reliable effects, thus ruling out a purely perceptual account of the observed priming effects (see Additional Figs. 1 and 2).

3.3. Discussion

Experiment 2 was designed to test the extent to which the early priming effect on Target productions within the Naming task in Experiment 1 was dependent on composition and lexical overlap. Our findings replicated the results of Experiment 1 in that activity localized in BA38 and BA20 was increased during prime production for combinatory as compared to non-combinatory primes in an early time-window, consistent with the presence of an early combinatory effect. Also, we replicated the early priming effect on target productions, with combinatory target productions that were lexically identical to their primes (*red boat – red boat*) eliciting reliably increased left anterior temporal activity than targets with no lexical overlap (*blue bell – red boat*). Our main question was whether this effect would be replicated

for single word prime-target pairs that were either the same or different (*bell – boat* vs. *boat – boat*). The answer was a clear ‘no’: the early LATL effect was specific to lexically identical *combinatory* pairs.

Having obtained evidence for structure dependence, we proceeded to test how much lexical overlap was necessary for this effect. A follow-up analysis of combinatory prime-target pairs showed that full lexical identity was not necessary. Instead, adjective overlap was sufficient. This pattern was obvious in BA20 and somewhat more gradient in BA38, though in both regions, only the main effect of Adjective was significant. Thus no evidence for the specialness of full overlap over just adjective overlap was obtained in either BA20 or BA38.

In sum, Experiment 2 effectively narrowed down the possible interpretations of the early priming effect in Experiment 1, showing that it does not extend to repetition priming of single words and that it does extend to combinatory prime-target pairs that share an adjective. Thus the effect appears to reflect an early planning stage of composition that is modulated by lexical identity of the first composing element.

4. General discussion

In this work we set out to address a very basic question about priming, namely whether it is possible to prime the composition of simple adjective-noun phrases, as reflected by previously studied MEG indices of basic composition. We discovered that these MEG activities can indeed be primed, but the presence of shared structure is not sufficient to drive the priming. Instead, our results show that priming is observed whenever the first element of the phrase, here the adjective, is shared between prime and target. Contrary to any prior literature on priming, we were able to measure the relevant computation in the same spatio-temporal location both during prime and target processing, thanks to the millisecond time resolution of MEG and the prior characterization of the combinatory effects in experiments involving no priming (e.g., Bemis & Pykkänen, 2011; Pykkänen et al., 2014). Both the combinatory effects on the primes and the priming effects on the targets were early, onsetting as early as ~100 ms after picture onset. Thus these effects likely reflect the very earliest stages of combinatory planning, such as the construction of the combinatory message. Indeed, our behavioral measurements did not track the observed LATL priming, instead mostly reflecting the degree of lexical overlap, a factor that should come into play later than message planning in production (Levitt, 1999).

Our priming effect identifies a new dependent measure for the study of priming that enables the investigation of processes just above the word level, i.e., the basic combination of words into larger units. Our finding suggests that at the earliest stages of combinatory planning, at around 100–150 ms after picture onset, a combinatory memory representation is formed that affects the planning of a relevantly similar combination on a subsequent trial. The timing of our effect fits in nicely with the model of language production proposed by Indefrey and Levelt (2004), in which 0–175 ms is defined as the stage of conceptual preparation (0–175 ms), followed by lemma retrieval and lemma selection (150–250 ms), phonological code retrieval (250–330 ms) and, finally, syllabification and articulation (400–600 ms; see also Hultén, Vihla, Laine, & Salmelin, 2009; Levitt, Praamstra, Meyer, Helenius, & Salmelin, 1998; Salmelin, Hari, Lounasmaa, & Sams, 1994; Sörös, Cornelissen, Laine, & Salmelin, 2003; Vihla, Laine, & Salmelin, 2006). Thus within this model, our effects fall within conceptual preparation as opposed to lemma-level processing, a conclusion that is also suggested by the result that shared structure was not sufficient to elicit the LATL priming effect. Crucially, our results show that the priming effect relates to conceptual processing *for the purpose of production*, given that primes that were not named did not elicit the effect.

The research program immediately opened up by our finding is characterizing exactly what counts as “relevantly similar” for the elicitation of the early LATL priming. Is the priming driven by a shared modifier, as has been proposed for relational priming in noun-noun compounds (Gagné, 2001; Gagné, 2002)? Or is it driven by a shared

first element in the phrase? A hypothesis based on firstness makes some intuitive sense given the earliness of the effect. Specifically, one could hypothesize that at 100 ms, as the visual properties of, say, a blue bell have been decoded in occipital regions, a message that is roughly of the form “blue something” has been constructed, with planning priority given to the lexical/conceptual element to be uttered first. When the just uttered prime production was also a blue something, elevated LATL amplitudes are elicited, perhaps indexing more efficient or better time-locked activity. Whether it is the modifier or phrase-initial status of the adjectives that drives the priming is of course a straightforwardly testable question given that languages vary in whether their adjectival modifiers are placed before or after the noun.

Given that the design of Experiment 1 also included shallower prime tasks than naming, with subjects simply viewing the primes either for the purpose of a perceptual or a slightly deeper “conceptual” task, we are able to rule out any purely perceptual explanations of the priming. Thus for example, our priming effect cannot reflect priming of color perception since such an effect should have been elicited in the View and Conceptual tasks of Experiment 1 as well. It is also interesting that the priming effect was driven by shared adjectives, given that in our prior studies, adjectives have served as non-combinatory control conditions, either as two-word lists (*red, blue*), or as single words (*red*) (Pykkänen et al., 2014). Thus outside a combinatory context, adjectives are a poor driver of LATL activity and crucially, do not engage the LATL more than single nouns (Exp. 2 in Pykkänen et al., 2014). Thus it is unlikely that the current finding could reflect adjective priming as opposed to combinatory priming driven by the shared adjective.

Throughout our study, the condition with structure sharing but no lexical overlap (*blue bell – red boat*) elicited the lowest LATL amplitudes during target processing, trending even lower than conditions involving non-combinatory primes (such as *boat – red boat* in Exp. 1 and *boat – boat* or *lamp – boat* in Exp. 2). Why should this be the case, if the observed activity in principle reflects combinatory processing? First, this pattern shows, as is already known from prior literature (e.g., Schwartz et al., 2009), that activating the LATL does not require a combinatory stimulus; single words activate it as well. However, in our study, single words did not elicit the early priming, showing that functionally, at around ~150 ms after picture onset, the LATL computes some type of combinatory operation as opposed to lexical/conceptual retrieval. Given the low amplitudes for the phrases involving no lexical overlap, it then appears that if in this time window, one needs to combine two concepts that have both been suppressed during prime production, LATL activity is also suppressed. The gist of this hypothesis is that the combinatory process is somehow disrupted or delayed if the input items both compete with the lexemes of the prime trial. In our behavioral results as well, the targets for the no-overlap combinatorial primes were always slower than the targets for the lexical non-combinatory primes, suggesting some type of inhibition.

As regards the consequences of the current results to functional interpretations of the combinatory LATL activity, our results converge well with prior findings on this region. Specifically, since pure structural overlap was not sufficient to elicit the LATL priming, this activity is unlikely to reflect purely structural operations. The same conclusion has been reached by a series of MEG experiments showing that combinatory effects in the LATL are robustly sensitive to the conceptual specificity of the composing items, a factor that should not affect syntactic composition (Westerlund & Pykkänen, 2014; Zhang & Pykkänen, 2015). Further, LATL composition effects are absent for numeral quantification (*two boats*), in which the composition does not add a conceptual feature to the noun but rather enumerates the number of tokens within a set (Blanco-Elorrieta & Pykkänen, 2016a; Del Prado & Pykkänen, 2014). On the basis of this body of work, the computational role of the LATL appears more consistent with some notion of conceptual combination than with either syntactic or semantic composition more generally (Pykkänen, 2015). Neuropsychological results on patients with LATL atrophy (Done & Gale,

1997; Hodges, Graham, & Patterson, 1995; Rogers et al., 2004; Rogers et al., 2006; Warrington, 1975) and corresponding hemodynamic research (Bright, Moss, Stamatakis, & Tyler, 2005; Moss, Rodd, Stamatakis, Bright, & Tyler, 2005; Rogers et al., 2006; Tyler et al., 2004) are also more consistent with a conceptual as opposed to a syntactic account of the LATL. However, as already mentioned above, LATL engagement is not limited to combinatory stimuli but rather, single words activate it as well. This is predicted by the influential semantic hub model of the LATL, which treats it as an amodal binding site for the distributed representations of concepts in general (Patterson, Nestor, & Rogers, 2007). However, when feature binding within individual concepts has been directly compared with feature binding across words that compose into a phrase, effects of composition have been clearly more robust than effects of the feature density (or conceptual specificity) of frequency matched single words (Westerlund & Pykkänen, 2014; Zhang & Pykkänen, 2015). This suggests that the LATL is strongly recruited for the creation of conceptual combinations while existing concepts only engage it weakly. In general the gist of this account conforms to the broader observation that cortical regions recruited for combinatory operations and lexical access appear to be largely overlapping (Fedorenko, Nieto-Castanon, & Kanwisher, 2012).

As regards the role of the LATL in conceptual combination, its activity profile makes it highly relevant for the relational priming literature on noun-noun combinations, with the current results of course adding to the convergence, given our modifier-driven priming effect (Gagné, 2001; Gagné, 2002). Exploring this connection further is another future line of research enabled by the current findings. Given that the relational priming literature is a comprehension literature, the first step would be to test the extent to which the current priming effect can also be elicited in comprehension, which of course is an independently important question. Since the presence of LATL combinatory effects in comprehension is well-documented (Bemis & Pykkänen, 2011; Bemis & Pykkänen, 2013a; Bemis & Pykkänen, 2013b; Brennan & Pykkänen, 2012; Westerlund & Pykkänen, 2014; Westerlund et al. 2015; Zhang & Pykkänen, 2015), such an extension is at least plausible. If the priming effect was elicited with a comprehension prime and a production target (contra production-to-production here), this would tell us that the priming is not dependent on the prime and target eliciting the same sequence of processing stages, given that the starting point in comprehension is form and in production, meaning. If the effect further extended to priming from comprehension to comprehension, this would tell us that it is not specifically related to speech planning at all and can extend to a situation in which the participant's role is in general purely reactive.

While we identified the left anterior temporal cortex as a combinatory site that shows priming, we also observed a lack of priming in nearby ventromedial prefrontal cortex, despite its sensitivity to the presence of composition both in this study and in prior work. This finding is important as it shows a reliable functional dissociation between left anterior temporal and ventromedial prefrontal areas despite the less than perfect spatial resolution of MEG and our specific localization methods (involving no individual MRIs). Thus on the basis of the current study, the answer to the question 'what combinatory activities can be primed?' would be that LATL activity can be primed but vmPFC activity cannot. While this answer is still preliminary, especially as regards the null finding in the vmPFC, the theoretically important question for future work is what type of functional differences could lead to such differences in priming. Since priming is fundamentally a phenomenon of memory, the natural conclusion from our finding would be that the LATL stores a relevant type of combinatory memory representations for priming whereas the vmPFC does not. This does not preclude the vmPFC from participating in composition, the hypothesis simply says a representation of the combination does not linger in this region, at least not long enough to last till the targets within a paradigm such as the current one. For a more detailed understanding of the possibly distinct combinatory memory representations in the LATL and the vmPFC, future work could for example vary the interval between prime and target.

5. Conclusion

This work characterized an early structure dependent priming effect in left anterior temporal cortex that was driven by adjective identity within minimal noun-adjective combinations. Thus our findings show that simple combinatory operations in minimal phrases can be primed, as measured by MEG, though the effect appears to be conceptual as opposed to purely structural in nature. In sum, these results provide novel evidence for the existence of structured memory representations that are created as a product of phrase production and opens a tractable research program to characterize the precise nature of these representations.

Acknowledgments

This research was supported by the National Science Foundation grant BCS-1221723 (LP), the National Institutes of Health grant R01 HD051030 (VSF), grant G1001 from the NYUAD Institute, New York University Abu Dhabi (LP) and La Caixa Foundation fellowship for Post-Graduate Studies (EBE).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.cognition.2017.09.010>.

References

- Adachi, Y., Shimogawara, M., Higuchi, M., Haruta, Y., & Ochiai, M. (2001). Reduction of non-periodic environmental magnetic noise in MEG measurement by continuously adjusted least squares method. *IEEE Transactions on Applied Superconductivity*, *11*, 669–672.
- Alario, F., Costa, A., & Caramazza, A. (2002). Frequency effects in noun phrase production: Implications for models of lexical access. *Language and Cognitive Processes*, *17*, 299–319.
- Balota, D. A., Yap, M. J., Hutchison, K. A., Cortese, M. J., Kessler, B., Loftis, B., ... Treiman, R. (2007). The English lexicon project. *Behavior Research Methods*, *39*(3), 445–459.
- Bar, M., Tootell, R. B., Schacter, D. L., Greve, D. N., Fischl, B., Mendola, J. D., ... Dale, A. M. (2001). Cortical mechanisms specific to explicit visual object recognition. *Neuron*, *29*(2), 529–535.
- Bemis, D. K., & Pykkänen, L. (2011). Simple composition: A magnetoencephalography investigation into the comprehension of minimal linguistic phrases. *The Journal of Neuroscience*, *31*, 2801–2814.
- Bemis, D. K., & Pykkänen, L. (2012). Combination across domains: An MEG investigation into the relationship between mathematical, pictorial, and linguistic processing. *Frontiers in Psychology*, *3*, 583.
- Bemis, D. K., & Pykkänen, L. (2013a). Basic linguistic composition recruits the left anterior temporal lobe and left angular gyrus during both listening and reading. *Cerebral Cortex*, *23*, 1859–1873.
- Bemis, D. K., & Pykkänen, L. (2013b). Flexible composition: MEG evidence for the deployment of basic combinatorial linguistic mechanisms in response to task demands. *PLoS ONE*, *8*(9), e73949.
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the royal statistical society. Series B (Methodological)*, *289*–300.
- Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex*, *19*(12), 2767–2796.
- Blanco-Elorrieta, E., & Pykkänen, L. (2015). Brain bases of language selection: MEG evidence from Arabic-English bilingual language production. *Frontiers in Human Neuroscience*, *9*.
- Blanco-Elorrieta, E., Ferreira, V. S., Del Prato, P., & Pykkänen, L. (2017). *The priming of basic combinatory responses in MEG*. Retrieved from osf.io/23sc8.
- Blanco-Elorrieta, E., & Pykkänen, L. (2016a). Composition of complex numbers: Delineating the computational role of the left anterior temporal lobe. *NeuroImage*, *124*, 194–203.
- Blanco-Elorrieta, E., & Pykkänen, L. (2016b). Bilingual language control in perception vs. action: MEG reveals comprehension mechanisms in anterior cingulate cortex and domain-general control of production in dorsolateral prefrontal cortex. *Journal of Neuroscience*, *36*(2), 290–301.
- Blanco-Elorrieta, E., & Pykkänen, L. (2017). Bilingual language switching in the lab vs. in the wild: The spatio-temporal dynamics of adaptive language control. *Journal of Neuroscience*, *37*, 9022–9036.
- Bock, J. K. (1986). Syntactic persistence in language production. *Cognitive Psychology*, *18*(3), 355–387.
- Boudewyn, M. A., Zirnstein, M., Swaab, T. Y., & Traxler, M. J. (2014). Priming

- prepositional phrase attachment: Evidence from eye-tracking and event-related potentials. *The Quarterly Journal of Experimental Psychology*, 67(3), 424–454.
- Branigan, H. P., Pickering, M. J., & McLean, J. F. (2005). Priming prepositional-phrase attachment during comprehension. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 31(3), 468.
- Brennan, J., & Pykkänen, L. (2008). Processing events: Behavioral and neuromagnetic correlates of aspectual coercion. *Brain and Language*, 106(2), 132–143.
- Brennan, J., & Pykkänen, L. (2010). Processing psych verbs: Behavioural and MEG measures of two different types of semantic complexity. *Language and Cognitive Processes*, 25(6), 777–807.
- Brennan, J., & Pykkänen, L. (2012). The time-course and spatial distribution of brain activity associated with sentence processing. *NeuroImage*, 60(2), 1139–1148.
- Bright, P., Moss, H. E., Stamatakis, E. A., & Tyler, L. K. (2005). The anatomy of object processing: The role of anteromedial temporal cortex. *The Quarterly Journal of Experimental Psychology Section B*, 58(3–4), 361–377.
- Brooks, T. L., & de Garcia, D. C. (2015). Evidence for morphological composition in compound words using MEG. *Frontiers in Human Neuroscience*, 9.
- Brown, M. W., & Aggleton, J. P. (2001). Recognition memory: What are the roles of the perirhinal cortex and hippocampus? *Nature Reviews: Neuroscience*, 2(1), 51.
- Copland, D. A., de Zubicaray, G. I., McMahon, K., & Eastburn, M. (2007). Neural correlates of semantic priming for ambiguous words: An event-related fMRI study. *Brain Research*, 1131, 163–172.
- Cuetos, F., Mitchell, D. C., & Corely, M. (1996). Parsing in different languages. Language processing in Spanish, eds. by Manuel Carreiras, José Garcia-Albea and Nuria Sebastián-Galles, 145–187.
- Del Prato, P., & Pykkänen, L. (2014). MEG evidence for conceptual combination but not numerical quantification in the left anterior temporal lobe during language production. *Frontiers in Psychology*, 5, 524.
- Devauchelle, A. D., Oppenheim, C., Rizzi, L., Dehaene, S., & Pallier, C. (2009). Sentence syntax and content in the human temporal lobe: An fMRI adaptation study in auditory and visual modalities. *Journal of Cognitive Neuroscience*, 21(5), 1000–1012.
- Done, D. J., & Gale, T. M. (1997). Attribute verification in dementia of Alzheimer type: Evidence for the preservation of distributed concept knowledge. *Cognitive Neuropsychology*, 14(4), 547–571.
- Egner, T., & Hirsch, J. (2005). Where memory meets attention: Neural substrates of negative priming. *Journal of Cognitive Neuroscience*, 17(11), 1774–1784.
- Fedorenko, E., Nieto-Castanon, A., & Kanwisher, N. (2012). Lexical and syntactic representations in the brain: An fMRI investigation with multi-voxel pattern analyses. *Neurophysiology*, 50(4), 499–513.
- Ferreira, V. S., & Slevc, L. R. (2007). AT the heart of the faculty of language are the processes of grammatical encoding. *The Oxford Handbook of Psycholinguistics*, 453.
- Ferreira, V. S., & Bock, K. (2006). The functions of structural priming. *Language and Cognitive Processes*, 21(7–8), 1011–1029.
- Gagné, C. L. (2001). Relation and lexical priming during the interpretation of noun–noun combinations. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 27(1), 236.
- Gagné, C. L. (2002). Lexical and relational influences on the processing of novel compounds. *Brain and Language*, 81(1), 723–735.
- Gagné, C. L., & Shoben, E. J. (2002). Priming relations in ambiguous noun–noun combinations. *Memory & Cognition*, 30(4), 637–646.
- Gagné, C. L., Spalding, T. L., & Ji, H. (2005). Re-examining evidence for the use of independent relational representations during conceptual combination. *Journal of Memory and Language*, 53(3), 445–455.
- Gagnepain, P., Chételat, G., Landeau, B., Dayan, J., Eustache, F., & Lebreton, K. (2008). Spoken word memory traces within the human auditory cortex revealed by repetition priming and functional magnetic resonance imaging. *The Journal of Neuroscience*, 28(20), 5281–5289.
- Genovese, C. R., Lazar, N. A., & Nichols, T. (2002). Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *NeuroImage*, 15(4), 870–878.
- Gilbert, J. R., Gotts, S. J., Carver, F. W., & Martin, A. (2010). Object repetition leads to local increases in the temporal coordination of neural responses. *Frontiers in Human Neuroscience*, 4, 30.
- Gotts, S. J. (2003). *Mechanisms underlying enhanced processing efficiency in neural systems*. Pittsburgh, PA: Carnegie Mellon University Press.
- Gotts, S. J., Chow, C. C., & Martin, A. (2012). Repetition priming and repetition suppression: Multiple mechanisms in need of testing. *Cognitive neuroscience*, 3(3–4), 250–259.
- Gross, J., Baillet, S., Barnes, G. R., Henson, R. N., Hillebrand, A., Jensen, O., ... Jensen, O. (2013). Good practice for conducting and reporting MEG research. *NeuroImage*, 65, 349–363.
- Hagoort, P., & Indefrey, P. (2014). The neurobiology of language beyond single words. *Annual Review of Neuroscience*, 37, 347–362.
- Haller, S., Radue, E. W., Erb, M., Grodd, W., & Kircher, T. (2005). Overt sentence production in event-related fMRI. *Neuropsychologia*, 43(5), 807–814.
- Hämäläinen, M. S., & Ilmoniemi, R. J. (1994). Interpreting magnetic fields of the brain: Minimum norm estimates. *Medical & Biological Engineering & Computing*, 32(1), 35–42.
- Hodges, J. R., Graham, N., & Patterson, K. (1995). Charting the progression in semantic dementia: Implications for the organization of semantic memory. *Semantic Knowledge and Semantic Representations*, 3(3–4), 463–495.
- Hultén, A., Vilha, M., Laine, M., & Salmelin, R. (2009). Accessing newly learned names and meanings in the native language. *Human Brain Mapping*, 30(3), 976–989.
- Indefrey, P., Brown, C. M., Hellwig, F., Amunts, K., Herzog, H., Seitz, R. J., & Hagoort, P. (2001). A neural correlate of syntactic encoding during speech production. *Proceedings of the National Academy of Sciences*, 98(10), 5933–5936.
- Indefrey, P., & Levelt, W. J. (2004). The spatial and temporal signatures of word production components. *Cognition*, 92(1), 101–144.
- Kotz, S. A., Cappa, S. F., von Cramon, D. Y., & Friederici, A. D. (2002). Modulation of the lexical–semantic network by auditory semantic priming: An event-related functional MRI study. *NeuroImage*, 17(4), 1761–1772.
- Kouider, S., De Gardelle, V., Dehaene, S., Dupoux, E., & Pallier, C. (2010). Cerebral bases of subliminal speech priming. *NeuroImage*, 49(1), 922–929.
- Lancaster, J. L., Rainey, L. H., Summerlin, J. L., Freitas, C. S., Fox, P. T., Evans, A. C., et al. (1997). Automated labeling of the human brain: A preliminary report on the development and evaluation of a forward-transform method. *Human Brain Mapping*, 5(4), 238.
- Lancaster, J. L., Woldorff, M. G., Parsons, L. M., Liotti, M., Freitas, C. S., Rainey, L., et al. (2000). Automated Talairach atlas labels for functional brain mapping. *Human Brain Mapping*, 10(3), 120–131.
- Ledoux, K., Traxler, M. J., & Swaab, T. Y. (2007). Syntactic priming in comprehension evidence from event-related potentials. *Psychological Science*, 18(2), 135–143.
- Leiken, K., & Pykkänen, L. (2014). MEG evidence that the LIFG effect of object extraction requires similarity-based interference. *Language and Cognitive Processes*, 29(3), 381–389.
- Levelt, W. J. (1999). Producing spoken language: A blueprint of the speaker. *The neuro-cognition of language* (pp. 83–122). Oxford University Press.
- Levelt, W. J. M., Praamstra, P., Meyer, A. S., Helenius, P. I., & Salmelin, R. (1998). An MEG study of picture naming. *Journal of Cognitive Neuroscience*, 10(5), 553–567.
- MacGregor, L. J., & Shtyrov, Y. (2013). Multiple routes for compound word processing in the brain: Evidence from EEG. *Brain and Language*, 126(2), 217–229.
- Marinkovic, K., Dhond, R. P., Dale, A. M., Glessner, M., Carr, V., & Halgren, E. (2003). Spatiotemporal dynamics of modality-specific and supramodal word processing. *Neuron*, 38(3), 487–497.
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG-and MEG-data. *Journal of Neuroscience Methods*, 164(1), 177–190.
- Menenti, L., Gierhan, S. M., Segaert, K., & Hagoort, P. (2011). Shared language: Overlap and segregation of the neuronal infrastructure for speaking and listening revealed by functional MRI. *Psychological Science*, 22(9), 1173–1182.
- Meyer, A. S. (1996). Lexical access in phrase and sentence production: Results from picture–word interference experiments. *Journal of Memory and Language*, 35, 477–496.
- Meyer, D. E., & Schvaneveldt, R. W. (1971). Facilitation in recognizing pairs of words: Evidence of a dependence between retrieval operations. *Journal of Experimental Psychology*, 90(2), 227.
- Meyer, D. E., & Schvaneveldt, R. W. (1976). Meaning, memory structure, and mental processes. *Science*, 192(4234), 27–33.
- Moss, H. E., Rodd, J., Stamatakis, E., Bright, P., & Tyler, L. K. (2005). Anteromedial temporal cortex supports fine-grained differentiation among objects. *Cerebral Cortex*, 15(5), 616–627.
- Neely, J. H. (1991). Semantic priming effects in visual word recognition: A selective review of current findings and theories. *Basic Processes in Reading: Visual Word Recognition*, 11, 264–336.
- Noppeney, U., & Price, C. J. (2004). An fMRI study of syntactic adaptation. *Journal of Cognitive Neuroscience*, 16(4), 702–713.
- Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience*, 8(12), 976–987.
- Pickering, M. J., & Branigan, H. P. (1998). The representation of verbs: Evidence from syntactic priming in language production. *Journal of Memory and Language*, 39(4), 633–651.
- Pickering, M. J., & Ferreira, V. S. (2008). Structural priming: A critical review. *Psychological Bulletin*, 134(3), 427.
- Poortman, E. B., & Pykkänen, L. (2016). Adjective conjunction as a window into the LATL's contribution to conceptual combination. *Brain and Language*, 160, 50–60.
- Porcaro, C., Medaglia, M. T., & Krott, A. (2015). Removing speech artifacts from electroencephalographic recordings during overt picture naming. *NeuroImage*, 105, 171–180.
- Price, A. R., Bonner, M. F., Peelle, J. E., & Grossman, M. (2015). Converging evidence for the neuroanatomic basis of combinatorial semantics in the angular gyrus. *The Journal of Neuroscience*, 35(7), 3276–3284.
- Pykkänen, L., Bemis, D. K., & Elorrieta, Blanco. (2014). Simple composition during language production in MEG. *Cognition*, 133, 371–384.
- Pykkänen, L. (2015). Composition of Complex Meaning: Interdisciplinary perspectives on the left anterior temporal lobe. In G. Hickok, & S. Small (Eds.). *Neurobiology of language* (1st ed.). NY: Elsevier.
- Pykkänen, L., Martin, A. E., McElree, B., & Smart, A. (2009). The anterior midline field: Coercion or decision making? *Brain and Language*, 108(3), 184–190.
- Pykkänen, L., & McElree, B. (2007). An MEG study of silent meaning. *Journal of Cognitive Neuroscience*, 19, 1905–1921.
- Ress, D., & Heeger, D. J. (2003). Neuronal correlates of perception in early visual cortex. *Nature Neuroscience*, 6(4), 414.
- Rogers, T. T., Hocking, J., Noppeney, U., Mechelli, A., Gorno-Tempini, M. L., Patterson, K., et al. (2006). Anterior temporal cortex and semantic memory: Reconciling findings from neuropsychology and functional imaging. *Cognitive, Affective, & Behavioral Neuroscience*, 6(3), 201–213.
- Rogers, T. T., Lambon Ralph, M. A., Garrard, P., Bozeat, S., McClelland, J. L., Hodges, J. R., et al. (2004). Structure and deterioration of semantic memory: A neuropsychological and computational investigation. *Psychological Review*, 111(1), 205.
- Rossell, S. L., Price, C. J., & Nobre, A. C. (2003). The anatomy and time course of semantic priming investigated by fMRI and ERPs. *Neuropsychologia*, 41(5), 550–564.
- Salmelin, R., Hari, R., Lounasmaa, O. V., & Sams, M. (1994). Dynamics of brain activation during picture naming. *Nature*, 368(6470), 463–465.
- Schoot, L., Menenti, L., Hagoort, P., & Segaert, K. (2014). A little more conversation – the

- influence of communicative context on syntactic priming in brain and behavior. *Frontiers in Psychology*, 5.
- Schriefers, H., De Ruiter, J. P., & Steigerwald, M. (1999). Parallelism in the production of noun phrases: Experiments and reaction time models. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, 25, 702–720.
- Schwartz, M. F., Kimberg, D. Y., Walker, G. M., Faseyitan, O., Brecher, A., Dell, G. S., et al. (2009). Anterior temporal involvement in semantic word retrieval: Voxel-based lesion-symptom mapping evidence from aphasia. *Brain*, 132(12), 3411–3427.
- Segaert, K., Menenti, L., Weber, K., Petersson, K. M., & Hagoort, P. (2012). Shared syntax in language production and language comprehension—An fMRI study. *Cerebral Cortex*, 22(7), 1662–1670.
- Segaert, K., Weber, K., de Lange, F. P., Petersson, K. M., & Hagoort, P. (2013). The suppression of repetition enhancement: A review of fMRI studies. *Neuropsychologia*, 51(1), 59–66.
- Sörös, P., Cornelissen, K., Laine, M., & Salmelin, R. (2003). Naming actions and objects: Cortical dynamics in healthy adults and in an amonic patient with a dissociation in action/ object naming. *NeuroImage*, 19(4), 1787–1801.
- Tooley, K. M., Traxler, M. J., & Swaab, T. Y. (2009). Electrophysiological and behavioral evidence of syntactic priming in sentence comprehension. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, 35(1), 19.
- Traxler, M. J. (2015). Priming of early closure: Evidence for the lexical boost during sentence comprehension. *Language, Cognition and Neuroscience*, 30(4), 478–490.
- Turk-Browne, N. B., Yi, D. J., Leber, A. B., & Chun, M. M. (2007). Visual quality determines the direction of neural repetition effects. *Cerebral Cortex*, 17(2), 425–433.
- Tyler, L. K., Stamatakis, E. A., Bright, P., Acres, K., Abdallah, S., Rodd, J., et al. (2004). Processing objects at different levels of specificity. *Journal of Cognitive Neuroscience*, 16(3), 351–362.
- Vihla, M., Laine, M., & Salmelin, R. (2006). Cortical dynamics of visual/semantic vs. phonological analysis in picture confrontation. *NeuroImage*, 33(2), 732–738.
- Warrington, E. K. (1975). The selective impairment of semantic memory. *The Quarterly journal of experimental psychology*, 27(4), 635–657.
- Weber, K., Lau, E. F., Stillerman, B., & Kuperberg, G. R. (2016). The yin and the yang of prediction: An fMRI study of semantic predictive processing. *PLoS One*, 11(3), e0148637.
- Westerlund, M., Kastner, I., Al Kaabi, M., & Pykkänen, L. (2015). The LATL as locus of composition: MEG evidence from English and Arabic. *Brain and Language*, 141, 124–134.
- Westerlund, M., & Pykkänen, L. (2014). The role of the left anterior temporal lobe in semantic composition vs. semantic memory. *Neuropsychologia*, 57, 59–70.
- Wible, C. G., Han, S. D., Spencer, M. H., Kubicki, M., Niznikiewicz, M. H., Jolesz, F. A., et al. (2006). Connectivity among semantic associates: An fMRI study of semantic priming. *Brain and Language*, 97(3), 294–305.
- Yuval-Greenberg, S., & Deouell, L. Y. (2009). The broadband-transient induced gamma-band response in scalp EEG reflects the execution of saccades. *Brain Topography*, 22.
- Zhang, L., & Pykkänen, L. (2015). The interplay of composition and concept specificity in the left anterior temporal lobe: An MEG study. *NeuroImage*, 111, 228–240.
- Ziegler, J., & Pykkänen, L. (2016). Scalar adjectives and the temporal unfolding of semantic composition: An MEG investigation. *Neuropsychologia*, 89, 161–171.