



# Lexical Access in Naming and Reading: Spatiotemporal Localization of Semantic Facilitation and Interference Using MEG

Julien Dirani<sup>1</sup> and Liina Pykkänen<sup>2</sup>

<sup>1</sup>New York University

<sup>2</sup>New York University and New York University Abu Dhabi

**Keywords:** lexical selection, naming, reading, semantic interference, MEG

## ABSTRACT

Naming an object involves quick retrieval of a target word from long-term memory. Research using the semantic interference paradigm has shown that objects take longer to name when they are preceded by primes in the same semantic category. This has been interpreted as reflecting either competition during lexical selection or as an interference effect at a later, postlexical level. Since the behavioral finding has been a core argument for the existence of competition during lexical selection in naming, understanding its processing level is important for models of language production. We used MEG to determine the spatiotemporal localization of the interference effect. We also compared its neural signature to the effect of semantic relatedness in reading, in which relatedness is expected to speed up behavioral responses and reduce activity in the left superior temporal cortex at around 200–300 ms. This is exactly what we found. However, in naming, we observed a more complex pattern for our semantically related targets. First, the angular gyrus showed a facilitory pattern at 300–400 ms, likely reflecting aspects of lexical access. This was followed by a broadly distributed and sustained interference pattern that lasted until articulatory stages. More transient interference effects were also observed at 395–485 ms in the left STG and at ~100–200 ms before articulation in the parietal cortex. Thus, our findings suggest that the semantic interference effect originates from both early and late sources, which may explain its varying localizations in previous literature.

## INTRODUCTION

Retrieval of words from memory is a core component of language production. The most common experimental and clinical paradigm for studying this process is object naming, a task in which a subject or patient is asked to produce the name of an object shown in a picture. Classic models of naming hypothesize this task to involve the lexical selection stage where related items compete with each other for selection (Bloem & La Heij, 2003; Levelt, 2001; Levelt, Roelofs, & Meyer, 1999). The main empirical evidence for the competition is a behavioral slow-down when a picture is preceded by a word prime from a related semantic category (e.g., dog preceding an image of a cat). Whether this effect originates at a lexical or postlexical level is, however, controversial.

Here we sought to characterize its neural sources in time and space with MEG. As a comparison task to naming, we chose overt reading (i.e., reading aloud), which also involves

Citation: Dirani, J., & Pykkänen, L. (2020). Lexical access in naming and reading: Spatiotemporal localization of semantic facilitation and interference using MEG. *Neurobiology of Language*, 1(2) 185–207. [https://doi.org/10.1162/nol\\_a\\_00008](https://doi.org/10.1162/nol_a_00008)

DOI:  
[https://doi.org/10.1162/nol\\_a\\_00008](https://doi.org/10.1162/nol_a_00008)

Supporting Information:  
[https://doi.org/10.1162/nol\\_a\\_00008](https://doi.org/10.1162/nol_a_00008)

Received: 28 August 2019  
Accepted: 19 March 2020

Competing Interests: The authors have declared that no competing interests exist.

Corresponding Author:  
Julien Dirani  
[julien.dirani@nyu.edu](mailto:julien.dirani@nyu.edu)

Handling Editor:  
Matthew Lambon Ralph

Copyright: © 2020 Massachusetts Institute of Technology. Published under a Creative Commons Attribution 4.0 International (CC BY 4.0) license.

articulation but should not evoke the behavioral interference effect since written words spell out the concept to be named, that is, the word selection process involves a word recognition rather than a word retrieval. As a way to diagnose whether neural effects reflected facilitation or interference, our design included a repetition priming condition, assumed to elicit only facilitatory effects. Thus, effects in the same direction as repetition priming were assumed to be facilitatory and effects in the opposite direction were assumed to be interfering.

Our general aim was to provide a basic characterization of the effects of semantic category relatedness in naming and overt reading, with a focus on the controversial lexical vs. postlexical question about relatedness effects in naming.

### The Picture-Word Interference Paradigm

On one account, lexical selection in production is considered a competitive process in which multiple candidates compete for selection (Levelt, 2001). Crucially, the speed and ease of lexical selection is affected by the activation level of the coactivated items. Core evidence for lexical selection by competition comes from picture-word interference (PWI) paradigms (Bloem & La Heij, 2003; Levelt et al., 1999), in which target pictures are named more slowly when preceded or superimposed by categorically related word primes (cat-dog) as compared with unrelated primes (chair-dog). The effect has been interpreted as a lexical-level effect where coactivated items (here “dog” and “cat”) compete for selection.

However, a number of subsequent findings have called into question the competitive nature of lexical selection. It appears that manipulating the type of semantic relation between the word prime and target could modulate priming effects. For instance, there is a reversal of the interference into a semantic facilitation with semantically related verb distractors (e.g., drive-car; Mahon, Costa, Peterson, Vargas, & Caramazza, 2007), with part-whole relations (e.g., engine-car; Costa, Alario, & Caramazza, 2005), with associates (carrot-rabbit; Heij, Dirx, & Kramer, 1990; Sailor, Brooks, Bruening, Seiger-Gardner, & Guterman, 2009; Xavier, Segui, & Ferrand, 2000) and with within-category close vs. within-category far distractor words (e.g., car-truck vs. wagon-truck; Mahon et al., 2007). Further, a facilitation effect is observed when primes are masked (Dhooge & Hartsuiker, 2010; Finkbeiner & Caramazza, 2006b).

Difficulties in reconciling these findings with the competitive account of lexical selection have led to the formulation of the response exclusion hypothesis (REH; Janssen, Schirm, Mahon, & Caramazza, 2008; Mahon et al., 2007), which is based on the premises that (a) language production involves a single-channel output buffer and that (b) written and auditory words have privileged access to this buffer over names of images (Mahon et al., 2007). Therefore, before the name of the image can be produced, this output buffer must be cleared of the representation of the prime. This process is regulated by semantic information (Glaser & Glaser, 1989; La Heij, 1988; Lupker, 1979) and gives rise to the interference effect. In other words, the REH argues that the competition originates postlexically, at the point when a decision about a response must be made. The competition is dependent on response-relevant criteria: for example, distractor verbs do not interfere with naming times of images because participants expect to have to name an object, making the verbs easier to exclude as potential responses (Mahon et al., 2007). Given the new evidence for a postlexical locus of semantic interference, the REH contends that lexical access is a noncompetitive process. Specifically, multiple candidates are activated during lexical access, but instead of competing for selection, the first candidate to reach a certain threshold is selected (Finkbeiner & Caramazza, 2006a, 2006b; Janssen et al., 2008). That is, according to the REH, the speed of lexical

selection is unaffected by coactivated candidates. It is worth mentioning that the REH explains facilitation effects (such as with carrot-rabbit relations) in terms of early priming at the lexical or conceptual level, which is outweighed by a late interference with response-relevant distractors only. Additional evidence in support of the REH and a noncompetitive lexical-access process comes from bimodal bilinguals who do not show cross-language semantic interference effects (Giezen & Emmorey, 2016). Since signed and spoken languages engage different articulators, this is taken as evidence for a postlexical, articulatory locus of semantic interference.

However, more recent studies failed to replicate the effect that motivated the REH. For instance, it appeared that the within-category close vs. within-category far effect could not be replicated, rather it was found that the inference increased as semantic distance got smaller (Fieder, Wartenburger, & Rahman, 2019; Rose, Aristei, Melinger, & Abdel Rahman, 2019). In addition, the part-whole facilitation effect was replicated at stimulus onset asynchronies (SOAs) of 150 ms and 300 ms, but not 0 ms (Sailor & Brooks, 2014). Other effects that were initially shown in support of the REH showed that they were actually in line with computational models of lexical selection by competition. For instance, the WEAVER++ model (Roelofs, 2003) supports lexical selection by competition and has shown to be able to account for distractor-frequency effects where low-frequency primes interfere more than high-frequency primes. Further, the model also accounted for the influence of a mask on the priming effects (Roelofs, Piai, & Schriefers, 2011).

#### **Stimulus Onset Asynchrony Modulates Priming Effects**

Previous studies have shown that manipulating SOA can modulate the priming effects in PWI tasks. Results from these studies show that the interference effect disappears with SOAs approaching 400 ms and longer (Bloem, van den Boogaard, & La Heij, 2004; Heij et al., 1990), with interference appearing to be the strongest at short SOAs, when the distractor is presented between –100 ms and 150 ms from the onset of the image (Costa et al., 2005; Heij et al., 1990; Sailor et al., 2009; Starreveld & La Heij, 1995; Xavier et al., 2000). It is then clear that a full account of interference and facilitation effects in priming should include a manipulation of SOA.

#### **Neural Correlates of the Semantic Interference and Facilitation Effects**

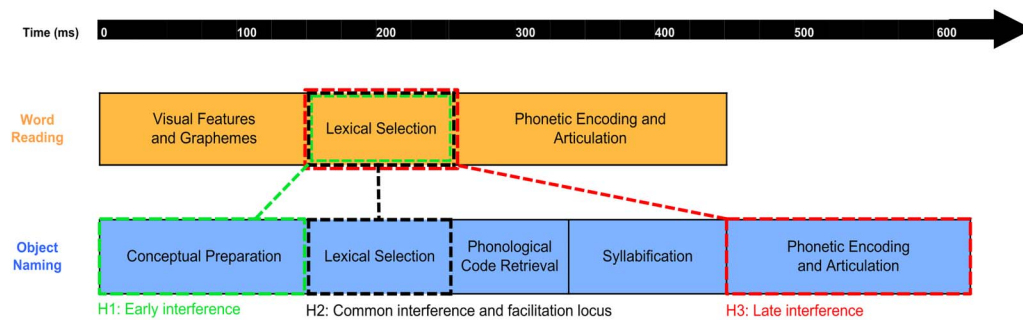
Determining the timing of semantic interference—specifically, whether competition occurs during lexical selection or at later stages of processing—is important for models of lexical access in production. Lexical selection is typically reported to start at around 200 ms (Indefrey, 2011; Munding, Dubarry, & Alario, 2016). Therefore, an early effect of semantic interference at ~200 ms would imply a lexical-level interference and competition for lexical access, while a later effect starting at ~400 ms would imply a postlexical effect and no competition during lexical access. Since electrophysiological measures have high temporal resolution, they can provide valuable information regarding the timing of the semantic interference. Different EEG studies have yielded variable timing estimates for the interference, showing both early (200–500 ms; Aristei, Melinger, & Abdel Rahman, 2011) and late (325–600 ms; Blackford, Holcomb, Grainger, & Kuperberg, 2012) onsets for the relevant effect. Additional EEG findings have also shown much later effects at 500–750 ms, which were interpreted as cognitive control mechanisms (Janssen, Hernández-Cabrera, van der Meij, & Barber, 2014). MEG measures showed a semantic interference effect at 350–650 ms in the left superior frontal gyrus in the 4–10 Hz range (Piai, Roelofs, Jensen, Schoffelen, & Bonnefond, 2014), however, an earlier

effect at 150–225 ms was found using a blocked semantic interference paradigm where images belonging to the same vs. different categories were presented in a blocked design (Maess, Friederici, Damian, Meyer, & Levelt, 2002). Further, an intracranial EEG study on epileptic patients showed that the interference effect was associated with an increase in activity in the supplementary motor area at both early (200–300 ms) and late (700–800 ms) time windows (Anders et al., 2019) and were interpreted as representing the initial conflict detection and later preresponse control during object naming. In essence, the semantic interference effect has been reported in various time windows ranging from 150 ms to 800 ms. A recent study has suggested an account of the semantic interference that is consistent across many different paradigms pointing to a lexical level locus (Roelofs, 2018). Nevertheless, the electrophysiological literature still does not show a consistent picture for the lexical locus of the semantic interference effect. It is therefore still unclear whether the semantic interference effect localizes at an early or a late time window, or at both.

Although the blood-oxygen-level dependent response is too slow to detect the timing of the interference effect, fMRI studies have provided information regarding the spatial extent of the effect. Semantic interference has modulated activity in the left posterior superior temporal gyrus (STG), left anterior cingulate cortex (ACC), bilateral orbitomedial prefrontal cortex, and the left midsection of the middle temporal gyrus (MTG) (de Zubicaray, Hansen, & McMahon, 2013; de Zubicaray, Wilson, McMahon, & Muthiah, 2001).

In contrast to naming, semantic relatedness has a straightforwardly facilitory effect in reading that is thought to originate at the lexical level via spreading activation from the prime to neighboring representations (Hala, Pexman, & Glenwright, 2007; Katz & Feldman, 1983; Rosson, 1983; Vinogradov, Ober, & Shenaut, 1992). To our knowledge, no study to date has examined the neural correlates of semantic facilitation in overt reading. In contrast, semantic priming has been extensively studied in silent reading, with lexical decision as the most common experimental task. The most consistent result from this work has been a reduction of the N400 response as a reflex of semantic priming, starting at around 250 ms and peaking at ~400 ms post-word onset (Holcomb & Anderson, 1993; Matsumoto, Iidaka, Haneda, Okada, & Sadato, 2005; Rossell, Price, & Nobre, 2003). The spatial extent of the effect involves the left inferior frontal gyrus, left STG and left MTG, the middle frontal gyri, the ACC, as well as at the inferior parietal lobe, as measured by hemodynamic methods (Kotz, Cappa, von Cramon, & Friederici, 2002; Matsumoto et al., 2005; Rissman, Eliassen, & Blumstein, 2003; Rossell et al., 2003).

While effects of semantic relatedness have been studied with neurobiological measures both in naming and reading (with most of the latter addressing silent reading), few studies to date have directly compared them (Anders et al., 2019). Such a comparison would provide crucial insight into the competitive vs. noncompetitive question in lexical access, because it allows for directly comparing the interference and facilitation effects in tasks that are maximally similar at the behavioral level. In the present study, we exploited the high temporal resolution of MEG to compare the spatiotemporal neural responses associated with facilitation priming in reading to semantic interference in naming. The relatively good spatial resolution of MEG also allowed us to complement the temporal data with spatial information, which in turn allowed us to examine the spatial extent of the interference and facilitation effects on the cortical surface. MEG does not provide the spatial resolution of fMRI, since it makes statistical estimates regarding the sources of the signal measured at the sensors. Nevertheless, given prior hypotheses regarding the source localization of effects, the spatial resolution of MEG offers a good estimate of the sources of the signal on the cortical surface. Here, if interference



**Figure 1.** Three contrasting hypotheses (H1, H2, H3) regarding the localization of semantic interference in object naming. Estimated times of processing steps are based on Indefrey and Levelt (2004).

effects in naming and facilitation effects in reading both localize in temporal areas (mainly STG and MTG) around 200–300 ms or earlier, this would conform to a shared lexical-level origin for the interference and facilitation effects. In contrast, if the interference effect in naming is manifested later than 400 ms after picture onset, a postlexical account of this effect is more likely (Figure 1). A lexical level of interference would be in line with models of lexical selection by competition, while a postlexical locus would imply that lexical selection is not competitive. Finally, a manipulation of SOA could provide us with additional insight as to the timing of priming effects. For instance, it is not clear how priming in reading would be affected, with possibly a facilitation effect turning into interference at a given SOA.

Importantly, the timing estimations that we are using (Figure 1) are based on Indefrey and Levelt's (2004) model of word production, which assumes a naming latency of 600 ms. Response times of participants vary from 600 ms, so these estimations can be inaccurate. To properly interpret the timing of our results, a proportional rescaling of the processing steps has been done, according to Roelofs and Shitova (2017). That is, each estimated processing step in the Levelt model is made longer or shorter depending on the average response time. For example, timing of lexical access is estimated to start at 200 ms for a naming time of 600 ms. For an observed naming time of 750 ms, the estimated timing of lexical access would have to be rescaled to be estimated to start at 250 ms ( $750/600 \times 200$ ).

## MATERIALS AND METHODS

### Participants

Thirty right-handed native English speakers were paid to take part in the study. Two participants were excluded due to excessive artifacts that resulted in >25% of rejected trials, and 3 participants were rejected due to equipment failure, leaving 25 good participants (14 female,  $M = 22.67$ ,  $SD = 5.55$ ). All participants had normal or corrected-to-normal vision and reported no history of neurological or language disorders. The study received ethical approval from the institutional review board at New York University Abu Dhabi.

### Experimental Design

The experiment consisted of an overt reading and an object naming task. The targets to be named consisted of line drawings (Object Naming) and lowercase words (Word Reading). In both tasks, three levels of primes were manipulated: First, semantically related primes



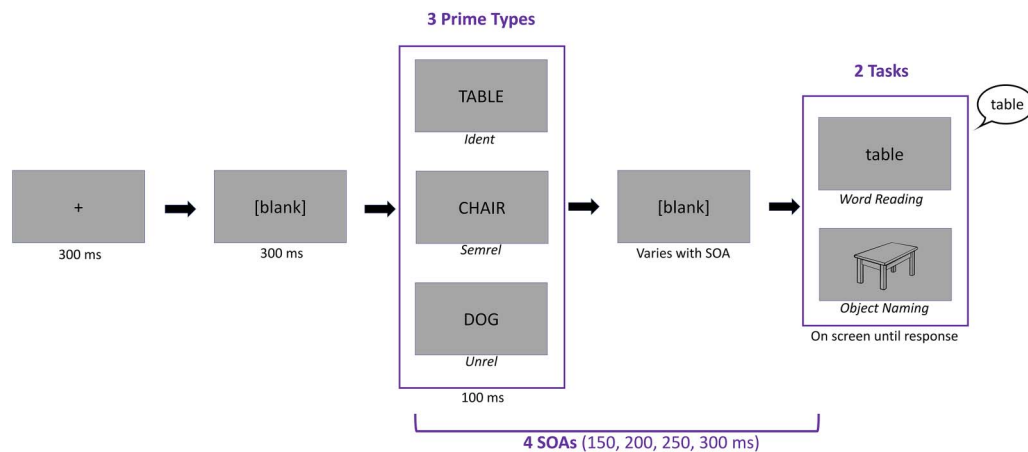
(Semrel, e.g., chair-table), which were words that belonged to the same semantic category of the targets. Categorically related primes have been shown to reliably induce interference effects in object naming. We therefore only used this type of semantic relation in order to guarantee we would observe the interference priming effect that we aimed to compare to facilitation in the reading task. We also used unrelated primes (Unrel, e.g., dog-table), which were words that differed from the target in all aspects (visual, phonology, and semantics). Finally, identical primes (Ident, e.g. table-table) repeated the target word or the word that would best name the object in the target image. We included this condition to provide us with a clear facilitation effect for both tasks, which would allow us to interpret the remaining effects in comparison. This is crucial for the neural data, where interpreting an increase or decrease in activation is not always straightforward. Crucially, Ident primes serve as the basis on which to discriminate between facilitatory and interfering neural patterns. Since identical prime-target pairs (table-table) are maximally related and expected to elicit robust facilitatory repetition priming, we considered a pattern facilitatory if the semantically related condition patterned between the unrelated and identical conditions. That is, the pattern is facilitatory if the semantically related condition patterned in the same direction as the identical condition, compared with the unrelated condition. In contrast, in an interference pattern, the semantically related condition should diverge from the unrelated condition in the opposite direction of the identical condition. For example, if the identical condition showed an increase in activation compared with the unrelated condition, a decrease in activation for the Semrel compared with the Unrel primes would be interpreted as an interference effect. All primes were in capital letters while all target words were in lowercase (e.g., TABLE-table) to control for purely visual priming.

We also manipulated the SOA at four different intervals: 150, 200, 250, and 300 ms. These SOAs were in the range that showed reliable interference effects in object naming (Heij et al., 1990; Sailor et al., 2009) and were chosen after undergoing a behavioral pilot of our experimental task aiming at selecting SOAs that would elicit a reliable interference effect in our design. This was done in order to successfully elicit an interference effect to properly assess the neural signature associated with it. Importantly, the potential interaction of SOA with Prime Type and Task could provide us with additional insight as to the timing of priming effects.

Stimuli were presented using Psychopy 1.84.2 (Peirce, 2007) on a screen positioned above the participants' heads while they laid back on a bed in the magnetically shielded room of the MEG. Each trial started with the presentation of a fixation cross that appeared for 300 ms, followed by a blank screen for 300 ms. Next, the prime appeared for 100 ms, followed by a blank screen. The duration of the prime was held constant, but the blank screen following it varied to create an SOA of 150, 200, 250, or 300 ms depending on the condition. Finally, the target remained on screen until the participants named it (Figure 2). Responses were recorded with a microphone positioned near the participant's mouth and the utterance times were recorded in real time using Psychopy's Voicekey.

### Stimuli

The lists of all primes and the list of targets were English nouns in their root form, balanced for length (Ident:  $M = 4.79$ ,  $SD = 1.41$ ; Unrel:  $M = 4.83$ ,  $SD = 1.22$ ; Semrel:  $M = 5.24$ ,  $SD = 1.29$ ) and frequency (Log frequencies: Ident:  $M = 9.12$ ,  $SD = 1.35$ ; Unrel:  $M = 9.03$ ,  $SD = 1.62$ ; Semrel:  $M = 8.28$ ,  $SD = 1.39$ ) across all lists. After the stimuli generation was done, 50 participants rated the semantic relation between the unrelated and semantically related primes and the targets via the Amazon Mechanical Turk platform ([www.mturk.com](http://www.mturk.com)). They



**Figure 2.** Trial structure and experimental design. SOA = stimulus onset asynchrony.

were instructed to rate how much they thought the words belonged to the same category using a Likert scale ranging from 1 to 5. Any prime-target pairs that had an average rating between 2.5 and 3.5 were excluded from the stimuli, creating two distinct groupings of semantically related and unrelated prime-targets (Semrel pairs:  $M = 4.31$ ,  $SD = 0.32$ ; Unrel pairs:  $M = 1.25$ ,  $SD = 0.19$ ).

The stimuli consisted of 82 Sets. Within each Set, there was one common target that was repeated six times: three times as an image and three times as a word. There were unique Semrel and Unrel primes for each of the target types. The Ident prime was repeated twice, once with each target type. Since we also wanted to manipulate SOA at four intervals (150, 200, 250, 300 ms), we opted to present each one of our Sets of stimuli (i.e., six prime-target pairs, with a shared target) twice. In order to control for anticipation and predictability, we created two versions of each prime type while trying to minimize the semantic distance between the two. In other words, each Set was presented twice and the versions of the primes were changed in each repetition. The result was that subjects saw each target 12 times (six times as an image, and six times as a word), and each unique prime twice (once before the image, and once before the word), with the exception of the Ident prime that was seen four times. In order to avoid confounding any effects of SOAs with effects created by specific items, it was necessary to avoid consistently pairing specific SOAs with specific Sets. That is, we had to counterbalance the pairing of SOAs with Sets across subjects. This was done by first arbitrarily splitting the 82 Sets into two lists of 41 Sets. Each list of Sets (A and B) was then paired with two SOAs, ensuring that each Set was presented twice (as previously stated). This pairing was counterbalanced across every six participants in order to ensure that a specific pairing of SOA to item did not confound the group-level results. Further, to control for the order of repetitions of targets within subjects, each of the 24 cells of the design was assigned to a block number following a Latin-squared method. Thus, the block number corresponded to the order of trials in the experiment. This was done to ensure that within each subject, the number of times that a given condition (e.g., Unrel, Object Naming, 150 ms SOA) appeared earlier in the experiment than another condition (e.g., Semrel, Word Reading, 200 ms SOA) was equal, pair-wise, across all conditions in the experiment. However, since the total number of cells in the design was 24 (6 prime-target pairs  $\times$  4 SOAs), while the total number of items in a List was 42, it was not possible to fully cross all of the conditions with block number (which would require

48 Sets per List, 96 in total). Thus, we distributed each of the conditions across block number in a manner that was as close to uniform as possible. Within the resulting 12 blocks, trial order was randomized, which conserved the Latin-squared order over the whole trials. There was a total of 41 trials per condition.

The downside of this randomization is that we repeated primes twice, over random pairs of SOAs. Ideally, we would have proceeded in one of the following two ways, but both were ultimately problematic: present every Set with all of the four SOAs (items would repeat excessively, potentially allowing participants to anticipate upcoming targets); or create completely unique Sets of stimuli for each SOA, balanced on relevant characteristics (unfeasible to generate enough unique Sets of prime-target pairs that could be controlled in all the necessary ways). The procedure that we used here was a compromise to minimize as much as possible the number of repetitions across SOAs, while counterbalancing the association of specific stimuli tokens with specific conditions.

### MEG Acquisition and Processing

Continuous MEG was recorded with a 208-channel axial gradiometer system (Kanazawa Institute of Technology) at a sampling rate of 1,000 Hz with an online band-pass filter of 0.1–200 Hz. The raw data was noise-reduced with the continuously adjusted least-squares method (Adachi, Shimogawara, Higuchi, Haruta, & Ochiai, 2001) using the MEG Laboratory software 2.004A (Yokogawa Electric and Eagle Technology Corp., Japan). All the following preprocessing was done using the MNE-Python 0.14 (Gramfort et al., 2014) and Eelbrain 0.25.2 (Brodbeck, 2017) packages. The data was first converted to .fif format. After visual inspection of the data, bad channels were excluded, and the data was low-pass filtered offline at 40 Hz. An independent component analysis was then fitted to the data using the “fastica” method, selecting components by 95 cumulative percentage of explained variance. Components related to eye-blinks, heartbeats, saccades, and dead channels were then rejected manually. Epochs from –100 to 600 ms from target onset were extracted and baseline correction was done using the 100 ms before the onset of the target. Epochs exceeding a maximum peak-to-peak threshold of  $\pm 2000$  femto-tesla were removed automatically, and the remaining epochs were scanned for eye-blink artifacts and were removed accordingly. It was not necessary to clean the data for articulation artifacts since correct responses never occurred before 600 ms after target onset. Finally, wrong responses, responses in which participants stuttered, and responses faster than 300 ms and slower than 2,000 ms were excluded from the analysis. For the naming task, responses that were a correct match with the picture but that were not in agreement with their word equivalent were excluded. For example, if the image depicted a “dog,” and a participant said “puppy,” it was considered a wrong response. All the remaining good epochs (Trials per condition across subjects:  $M = 956.5$ ,  $SD = 29.5$ ) were down-sampled by 5, so that the sampling rate became 200 Hz, and were then averaged by condition to form the evoked responses.

Each subject’s head-shape was created using an optical FastSCAN scanner (Polhemus) and was co-registered with the FreeSurfer (<http://surfer.nmr.mgh.harvard.edu/>) average brain. To execute a better co-registration, the average brain was scaled using three-dimensional axes to match each subject’s head-shape. The source space was defined as a dipole grid on the white matter surface using the topology of a recursively subdivided icosahedron (“ico-4” option). Only sources in the left hemisphere were included and were defined using the PALS-B12 atlas (Van Essen, 2005). A separate inverse solution was then computed for each subject with the evoked responses, using the forward solution as well as the noise covariance matrix



computed from the respective 100 ms baselines of each condition. For each subject, the noise covariance matrix was estimated using the best estimator out of the three methods shrunk covariance, diagonal fixed covariance, and empirical covariance, based on log-likelihood and cross-validation on unseen data (Engemann & Gramfort, 2015). For each source location, minimum norm current estimates were computed using three orthogonal dipoles, resulting in a 3D vector. Only the lengths of the vectors were retained, resulting in orientation-free source estimations. The resulting estimates were noise-normalized at each source using a signal-to-noise ratio regularization factor of 3 for the regularization of the inverse operator. This resulted in noise-normalized statistical parametric maps, which were then converted to dynamic maps (dSPMs) and provided information about the statistical reliability of the estimated signal at each source (Dale et al., 2000). Finally, source activity was morphed to the FreeSurfer average source space in order to be comparable across subjects.

### Statistical Analyses

#### *MEG stimulus-locked analyses*

The initial statistical analysis was based on a mass univariate analysis with spatiotemporal cluster-based permutation tests (Holmes, Blair, Watson, & Ford, 1996; Maris & Oostenveld, 2007) applied to the source estimates (in dSPMs). Average source estimates for each condition and for each subject were used in the analysis. The  $F$  value of a  $2 \times 3 \times 4$  repeated-measures ANOVA (Task  $\times$  Prime Type  $\times$  SOA) was computed for each source at each time point in the full left hemisphere and limited to the 100–600 ms time window. This  $F$  map was thresholded at an  $F$  value corresponding to an uncorrected  $p$  value of 0.01. Clusters were formed based on direct adjacency in space and time, with the restrictions that they contain a minimum of 10 sources and last at least 10 ms. The sum of all  $F$  values ( $\Sigma F$ ) was computed for each resulting cluster. This procedure was then repeated 10,000 times, each time with a random permutation of the data, by shuffling condition labels within subjects. For each permutation, the largest of the  $\Sigma F$  was saved to create a nonparametric permutation distribution. The Monte Carlo  $p$  value was computed for each cluster in the original  $F$  map as the proportion of random permutations in which the observed  $\Sigma F$  was larger than the values from the permutation distribution. We retained clusters whose Monte Carlo  $p$  value was smaller or equal to 0.05.

A secondary analysis was performed to unpack the patterns of priming effects within each Task. The same cluster-based permutation test described above was performed, sub-setting the data by Task and thus using a  $3 \times 4$  repeated-measures ANOVA (Prime Type  $\times$  SOA). The Monte Carlo  $p$ -value threshold was corrected using the Bonferroni method to account for the multiple comparisons across the two tasks.

#### *MEG response-locked analysis*

Electrophysiological data is most often analyzed time-locked to the onset of the stimulus (Indefrey, 2011). While it has proven to be very useful, this approach is not ideal to assess the later processing steps of language production, mainly the planning of the articulation. In fact, activity that is related to the execution of the response tends to be reduced in stimulus-locked analyses (Riès, Janssen, Burle, & Alario, 2013). In the current study, one of our hypotheses predicts that the semantic interference effect localizes at later motor preparatory stages of processing, which makes it crucial to properly assess the stages right before the articulation occurs. Thus, it was essential to include an analysis with epochs locked at the response time.

For each trial, the utterance time was taken along with the 600 ms preceding it to create epochs of equal length. One additional subject was excluded from this analysis due to excessive noise in the MEG data (>25% of trials rejected), resulting in a sample of 24 participants. Baseline correction was done using the 100 ms before the onset of the prime, and source reconstruction was estimated using the similar procedure described in “MEG acquisition and processing.” Finally, the same spatiotemporal within-task  $3 \times 4$  ANOVA (Prime Type  $\times$  SOA) that was previously mentioned was run on the response-locked source-level epochs.

#### **Plots and assumptions of MEG results**

For all analyses, significant clusters were plotted as time courses as well as bar graphs showing their average dSPM value. Sources included in the cluster were plotted on the FsAverage brain with the average  $F$  values for the time window of the significant cluster. In all plots, time 0 represented the onset of the target. Concerning results for the effect of Prime Type, we only reported clusters showing a semantic priming pattern. That is, we only presented clusters where the Semrel and Unrel conditions showed distinct time courses that separate from each other. The reason is that pure Ident priming effects do not directly address our hypothesis, since the Ident condition was only included as a baseline for interpreting semantic priming effects.

It is important to mention an assumption that goes into plotting clusters found using spatiotemporal permutation tests. In the spatiotemporal test, a significant cluster is a set of contiguous points in the time-source domain. That is, not all sources contribute equally to the cluster at all time points, which makes it difficult to visualize the spatiotemporal cluster as a continuous time course. The most straightforward way to visualize the cluster is to average over all the sources (in space) and plot the resulting average activation over time, which assumes all sources contribute equally to the cluster at all time points. Crucially, as a consequence, we cannot visually deduct from the plotted time course anything that is outside the cluster's time extent because we do not have a priori information that any effect survived the multiple comparison there. We can interpret the activation in the cluster time window because we confidently know that there is an effect there that survived the permutation test, even though the plot is susceptible to smearing out information in space and time.

#### **Behavioral Analyses**

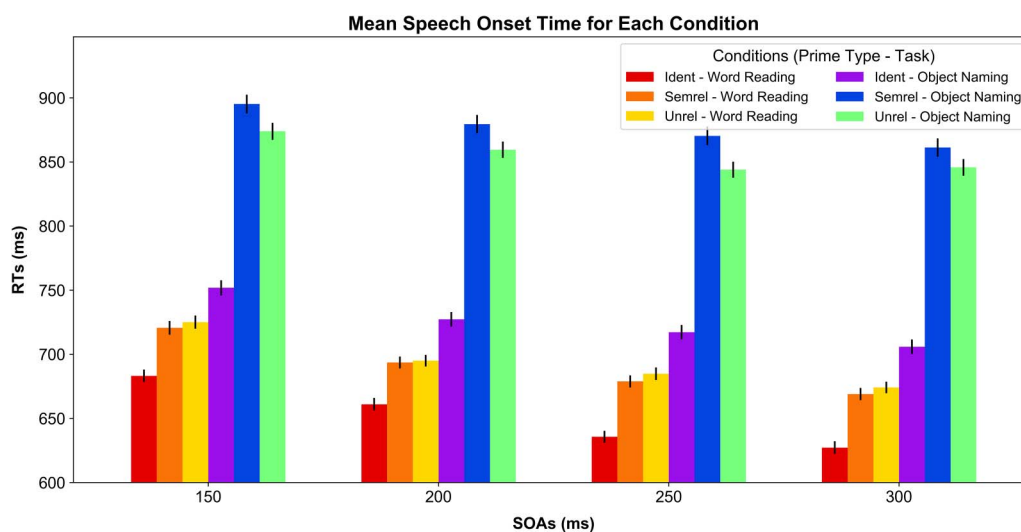
Voice utterance reaction times (RTs) were analyzed with a linear mixed-effect model using the LmerTest package (Kuznetsova, Brockhoff, & Christensen, 2017) in R (R Core Team, 2013). As with the MEG data, wrong responses, responses in which participants stuttered, and responses faster than 300 ms and slower than 2,000 ms were excluded from the analysis. The initial model included all main effects of Prime Type, Task, SOA, all two-way interactions, and the three-way interaction as fixed effects. Random intercepts were used for subjects and items. To test for the significance of the predictors, we performed a sequential decomposition of the contributions of the fixed effects using the ANOVA function from the LmerTest package, using type-III hypothesis test. For each predictor, an  $F$  test and its corresponding  $p$  value were estimated using Satterthwaite's method (Giesbrecht & Burns, 1985; Hrong-Tai Fai & Cornelius, 1996). Post hoc pairwise comparisons of significant effects were done using differences of least square means corrected for multiple comparisons using the Tukey method, with Satterthwaite's estimation for degrees of freedom. The final model was then retrieved with backwards elimination of nonsignificant effects.

## RESULTS

## Behavioral Data

We found a main effect of Task,  $F(1, 23,382) = 5,585.43, p < .001$ , with longer RTs observed for Object Naming ( $M = 817.63, SD = 211.25$ ) compared with Word Reading ( $M = 679.04, SD = 156.10$ ; Figure 3). We also found a main effect of Prime Type,  $F(2, 23,378) = 1,053.39, p < .001$ , showing that the Ident priming condition was the fastest ( $M = 688.25, SD = 172.55$ ), followed by Unrel ( $M = 773.51, SD = 194.98$ ) and then Semrel ( $M = 779.79, SD = 210.62; p < .001$  for all post hoc paired tests).

Further, we found an interaction between Task and Prime Type,  $F(2, 23,377) = 326.16, p < .001$ , which showed that, in Object Naming, RTs were shorter for Unrel ( $M = 855.76, SD = 200.16$ ) compared with Semrel primes ( $M = 876.48, SD = 219.71; p < .001$ ), illustrating the predicted semantic interference effect. In contrast, for Word Reading, RTs were shorter for Semrel ( $M = 690.57, SD = 155.46$ ) compared with Unrel primes ( $M = 694.91, SD = 153.06$ ), although this effect was not significant ( $p = 0.21$ ). This could be due to the fact that in overt reading, as opposed to silent comprehension tasks, participants can rely on phonological and orthographic information, and less on semantics, thus decreasing the strength of the semantic facilitation effect. Further, the Ident priming condition revealed the fastest RTs in both tasks (In Object Naming:  $M = 727.51, SD = 180.39$ ; In Word Reading:  $M = 651.79, SD = 156.53$ ). The main effect of SOA was a reliable predictor of RTs,  $F(3, 14,703) = 56.21, p < .001$ ; SOA 150:  $M = 772.26, SD = 200.35$ ; SOA 200:  $M = 750.47, SD = 194.43$ ; SOA 250:  $M = 735.61, SD = 195.06$ ; SOA 300:  $M = 728.31, SD = 197.71$ , and also interacted with the effect of Task,  $F(3, 23,378) = 2.8817, p < .05$ . Within each task, RTs got shorter as SOAs got longer (In Object Naming: SOA 150:  $M = 838.63, SD = 213.03$ ; SOA 200:  $M = 820.95, SD = 209.75$ ; SOA 250:  $M = 808.39, SD = 208.48$ ; SOA 300:  $M = 802.77, SD = 212.01$ . In Word Reading: SOA 150:  $M = 709.69, SD = 164.74$ ; SOA 200:  $M = 683.17, SD = 150.39$ ; SOA 250:  $M = 666.43, SD = 151.96$ ; SOA 300:  $M = 656.72, SD = 151.68$ ), with the exceptions of



**Figure 3.** Behavioral RTs (i.e., utterance onset times) across all conditions. A stable effect of Prime Type was observed in both Word Reading (warm colors) and Object Naming (cool colors) across all SOAs. RT = reaction time; SOA = stimulus onset asynchrony.

SOAs 250 and 300 in the Object Naming task, in which cases RTs did not significantly differ ( $p = .20$ ).

The final model that was obtained with backwards elimination of nonsignificant effects is presented below. RTs were significantly predicted by the main effects of Prime Type and SOA, as well as the interaction of Task with both Prime Type and SOA. Items and subjects were included as random factors.

$$RT \sim \text{Task} + \text{PrimeType} + \text{SOA} + \text{Task} : \text{PrimeType} + \text{Task} : \text{SOA} + (1|\text{Subject}) + (1|\text{Item})$$

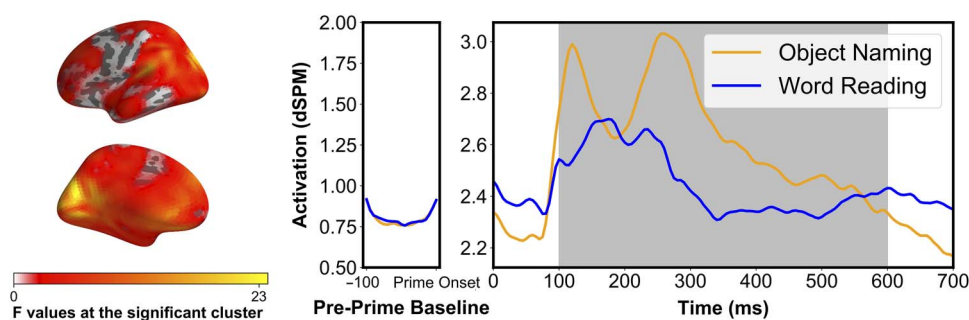
## MEG Data

### Omnibus analysis

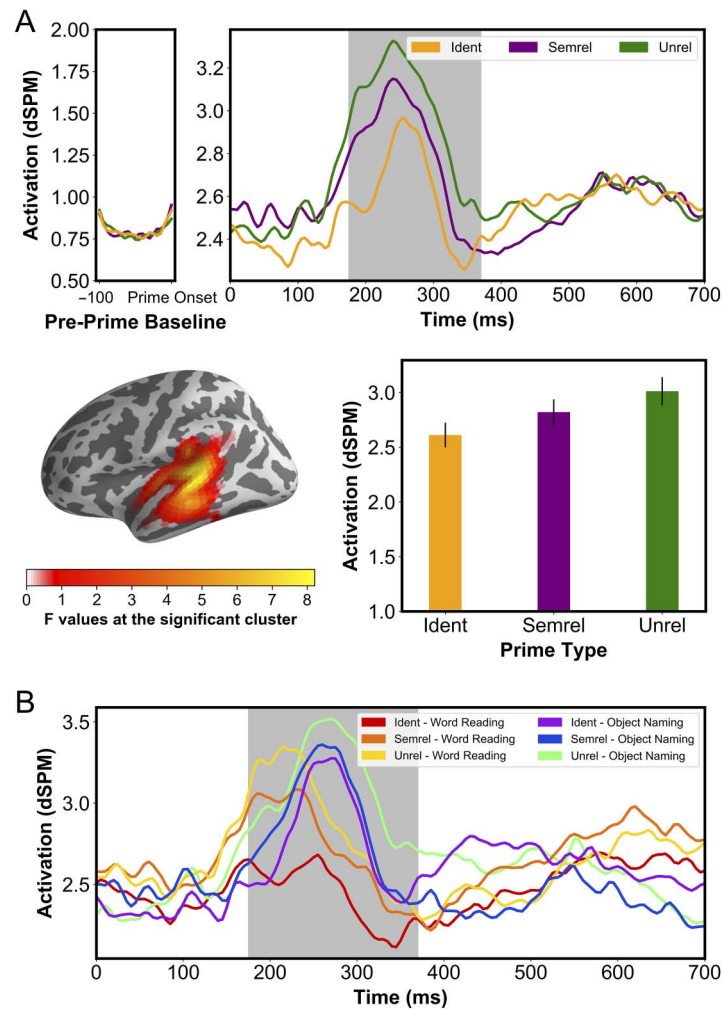
The omnibus cluster-based permutation test revealed a robust, widespread main effect of Task. The biggest spatial cluster expanded on most of the left hemisphere (93.72%, 2,401 sources) and lasted for the full analysis time window (100–600 ms,  $p < .001$ ; Figure 4). In addition, the time courses of the two tasks exhibited two drastically different patterns. This indicates that Word Reading and Object Naming were associated with strikingly different neural signatures across the better part of the left hemisphere.

We also found a spatiotemporal cluster for the main effect of Prime Type (Figure 5) showing a priming effect localized to the middle STG, between 175 ms and 370 ms ( $p < .001$ , in which activation increased stepwise as semantic distance increased. This pattern followed that of the behavioral results collapsed over Task and SOA in which RTs were shortest for Ident primes and longest for Unrel primes. The effect of Prime Type did, however, interact with the effect of Task (Figure 6), indicating that the priming pattern described above might be a generalization that is not necessarily representative of the priming patterns within each task. For Object Naming, the priming pattern was in line with that of the behavioral results, with the highest activation for the Ident primes, followed by the Unrel primes and then the Semrel primes. For the Word Reading task, the activation of the Semrel condition appeared higher than that of Unrel and Ident priming conditions, however, the latter two had similar activation levels.

Finally, we found that SOA modulated brain responses at six different spatiotemporal clusters (Figure 7). The largest cluster contained 518 sources located in frontal areas as well as



**Figure 4.** A widespread main effect of Task extending through the entire analysis time window and almost the entire left hemisphere (as well as the right hemisphere, as observed in an additional post hoc test;  $p < 0.05$ , corr., with the most reliable signal centered at medial occipital areas. The large effect of Task motivated our within-task analyses, to achieve greater sensitivity to observe priming effects. dSPM = dynamic statistical parameter map.



**Figure 5.** Main effect of Prime Type in the full across-tasks analysis. (A) Spatial extent of the significant cluster (left) and its time course averaged across tasks. Bar graph shows mean amplitudes of the significant (shaded) temporal cluster across priming conditions. (B) Same data split by task, revealing a clearer stepwise amplitude reduction for Word Reading than for Object Naming. (Grey shading on time courses indicates  $p < 0.05$ , corr.). dSPM = dynamic statistical parameter map; Ident = identical; Semrel = semantically related; Unrel = unrelated.

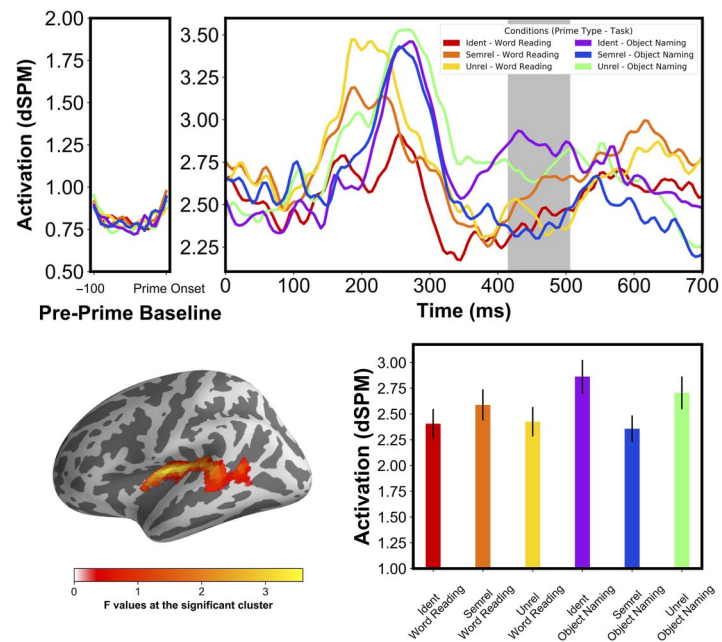
anterior medial temporal areas ( $p < .001$ ) and showed a stepwise increase in activation as SOAs got longer.

#### Analysis within task

Our primary goal was to unpack the neural signatures of semantic priming for Object Naming and Word Reading. Because the main effect of Task was so dramatic, with 93.72% of the left hemisphere modulated by Task for the whole analysis time window, we opted for a second analysis within Task. Our motivation was to exclude the large effect of Task in order to gain a better understanding of semantic priming within each task.

With this second analysis, we were able to observe distinct priming patterns for each task (Figure 8A–D). For the Object Naming task, we found an early facilitation effect at 310–380 ms followed by an interference effect at 395–485 ms. The facilitation was localized in sources

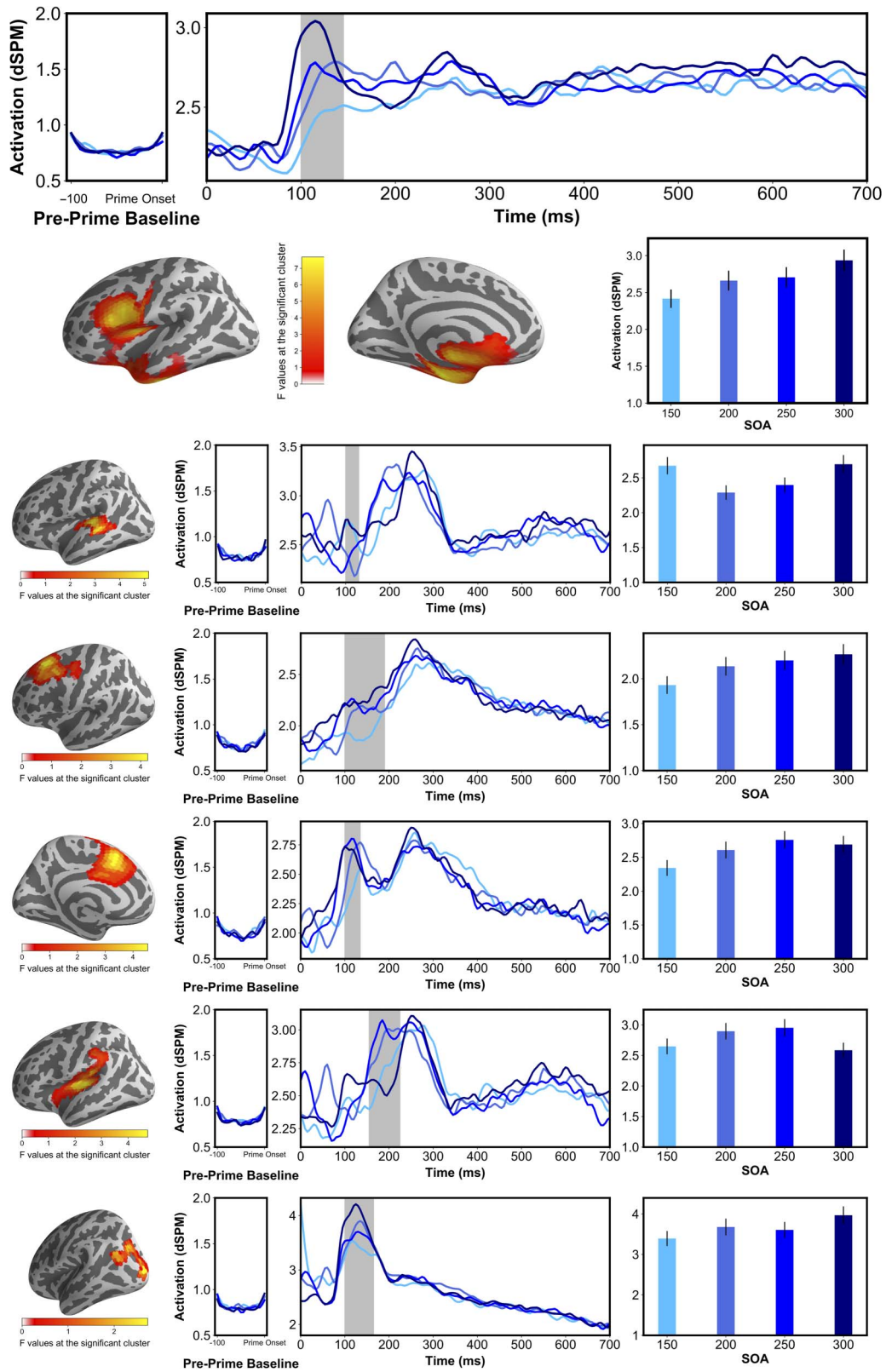




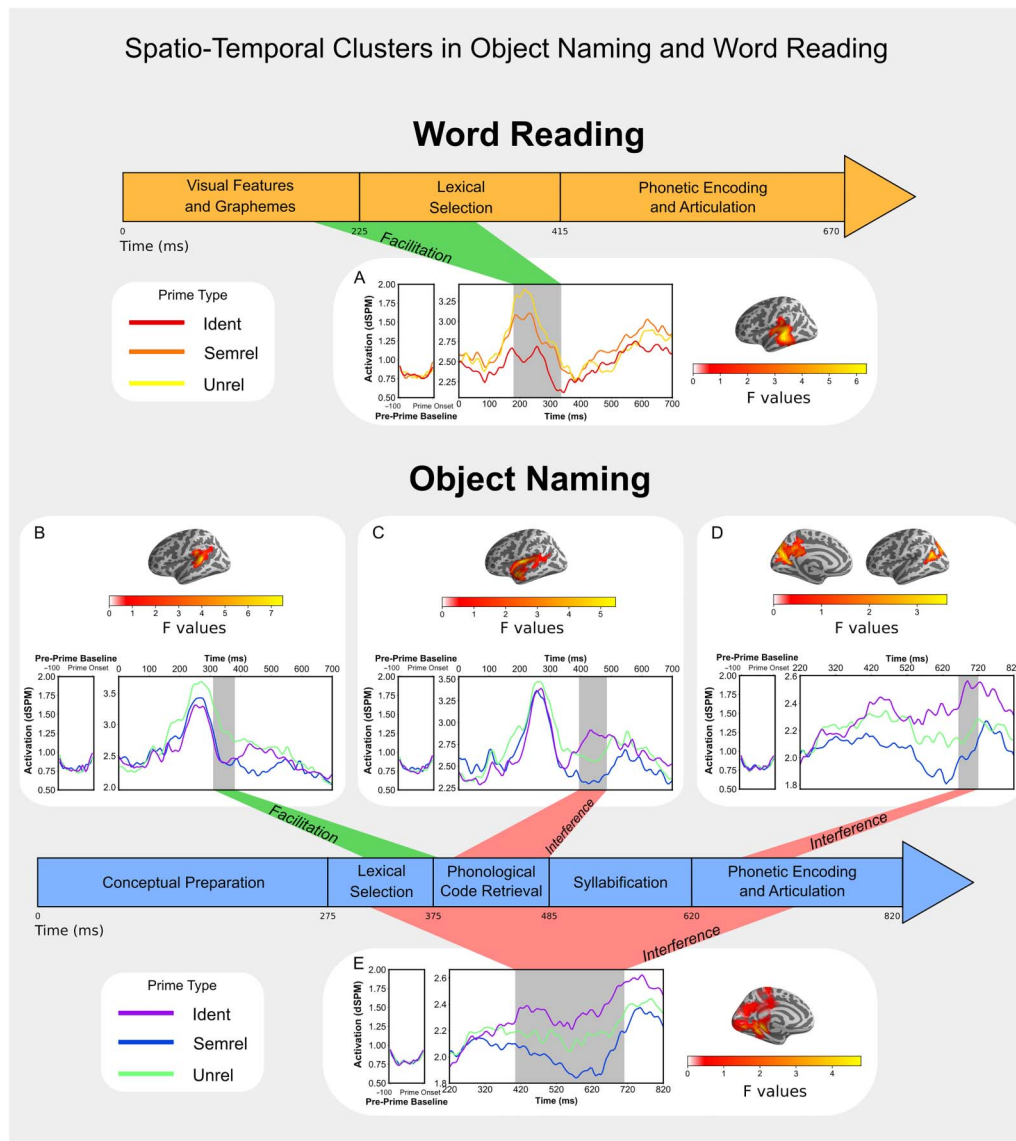
**Figure 6.** Interaction cluster between Task and Prime Type in the full across-tasks analysis, showing an amplitude reduction for the semantically related condition in the Object Naming task only ( $p < 0.05$ , corr.). dSPM = dynamic statistical parameter map; Ident = identical; Semrel = semantically related; Unrel = unrelated.

in the angular gyrus area and posterior parts of the STG. Surprisingly, this facilitation effect did not show any significant distinction between the Semrel and Ident priming conditions. That is, this priming effect did not distinguish between related pairs and identical pairs. Crucially, we also found in Object Naming a late cluster at 395–485 ms ( $p < .001$ ), localizing at the anterior STG and the insular cortex. We observed that the identical and semantically related conditions separated in opposite directions from the unrelated condition, with higher activation for Ident and lower for Semrel primes. Specifically, there was a decrease in activation for the Semrel priming condition compared with the Unrel condition and, importantly, an increase in activation with Ident primes that elicited a strong facilitation effect in the behavioral data, representing overall a semantic interference pattern. This pattern is in line with RT results where Ident primes elicited the fastest responses, followed by Unrel and then finally Semrel primes. Crucially, the priming pattern observed was different in the Word Reading task, where we found an early facilitation priming pattern between 180–335 ms ( $p < .001$ ) at the middle STG and expanding to the middle MTG (Figure 8A). We observed a stepwise increase in activation as semantic distance increased, which is typical of facilitatory priming (Bentin, McCarthy, & Wood, 1985; Holcomb, 1988). This pattern is once again in line with the observed RTs. This cluster appeared to be very similar to the cluster in Figure 5A, which indicates that the stepwise priming effect found in the first analysis was likely driven by the Word Reading task alone, especially since the second analysis did not find a similar pattern in Object Naming.

Finally, there was a main effect of SOA for both tasks (Figure 9). In Object Naming, we found four clusters modulated by SOA, all occurring early, before 200 ms. All of the clusters seemed to exhibit the pattern that was observed in the behavioral data, with a stepwise increase in activation as SOAs got longer. In Word Reading, the posterior part of the insular



**Figure 7.** Omnibus analysis: Spatiotemporal clusters for the main effect of SOA. The shaded regions indicate that the difference in activity between the conditions was significant at  $p < 0.05$ . dSPM = dynamic statistical parameter map; SOA = stimulus onset asynchrony.

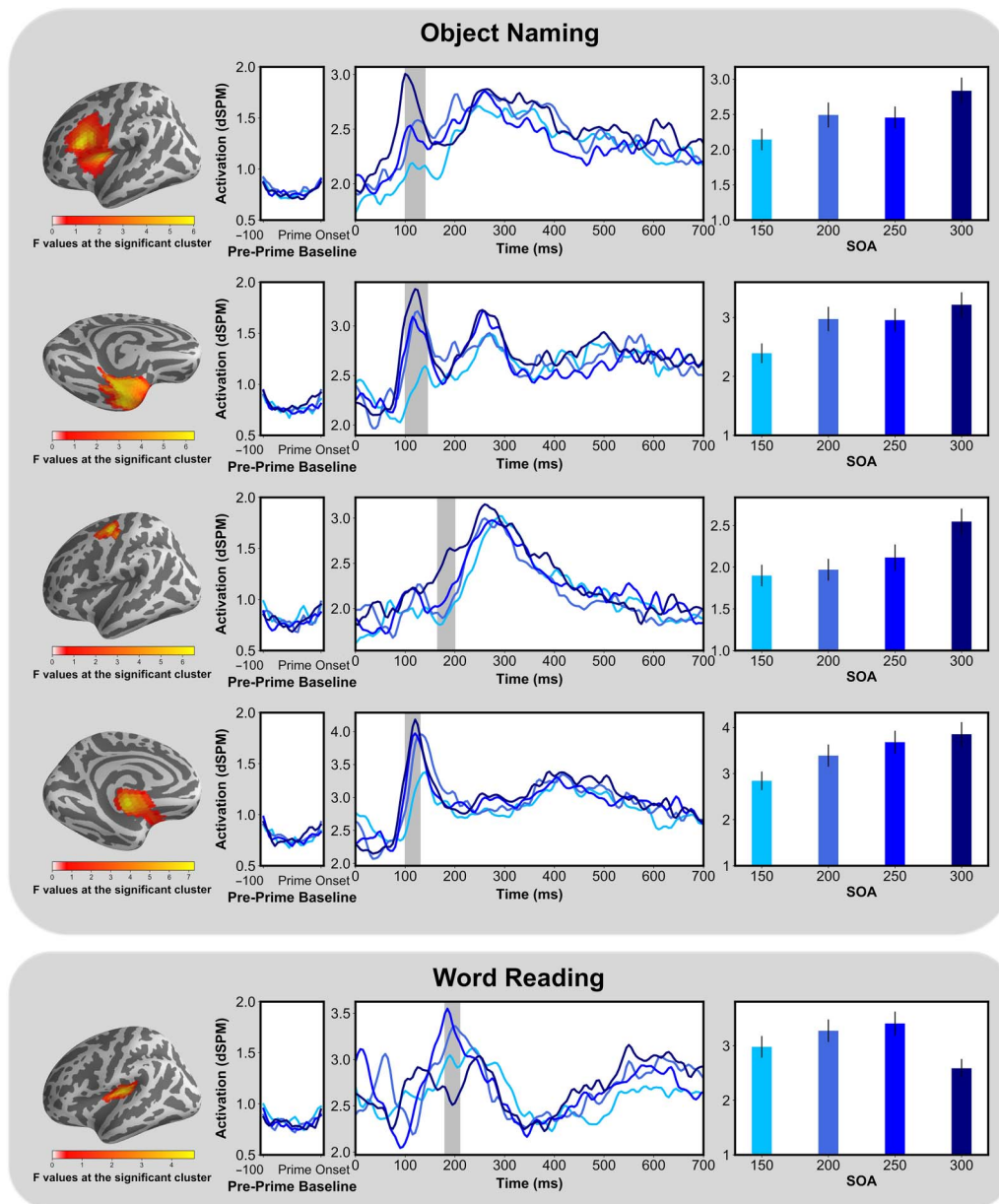


**Figure 8.** Within-task analysis of priming effects, showing a stepwise amplitude reduction (Ident < Semrel < Unrel) in the Word Reading task (A) centered around the left STG ( $p < 0.05$ , corr.). In Object Naming (bottom) we see an earlier amplitude reduction for the semantically related and identical conditions in the angular gyrus (B) followed by a later interference pattern (Semrel < Unrel < Ident) around the STG (C). The response-locked effects show an amplitude reduction for the semantically related condition localized at the anterior part of the intraparietal sulcus at  $-100$  ms (D) and in the posterior part of the parahippocampal gyrus starting at  $-400$  ms until  $-100$  ms, with the semantically related condition peaking at  $-200$  ms (E). Estimated times of processing steps are based on Indefrey and Levelt (2004) and are scaled proportionally to our observed average reaction times for each task, according to Roelofs and Shitova (2017). dSPM = dynamic statistical parameter map; Ident = identical; Semrel = semantically related; Unrel = unrelated; STG = superior temporal gyrus.

cortex appeared to be modulated by SOA at 180–210 ms. The activations at this cluster did not seem to follow a straightforward pattern.

#### Response-locked analysis within task

For the Word Reading task, we did not find any semantic facilitation effects in the speech-locked analysis. In Object Naming, we found two clusters with distinct time courses for all



**Figure 9.** Analysis within task: Spatiotemporal clusters for the main effect of SOA, within task. The shaded regions indicate that the difference in activity between the conditions was significant at  $p < 0.05$ . dSPM = dynamic statistical parameter map; SOA = stimulus onset asynchrony.

three priming conditions. The first cluster was located at the anterior part of the intraparietal sulcus at  $-150$  to  $-100$  ms prior to the utterance time. The second cluster started at  $-400$  ms until  $-100$  ms and peaked at  $-200$  ms before utterance and spread on the posterior part of the parahippocampal gyrus (Figure 8D–E).

## DISCUSSION

Here we took advantage of the spatiotemporal resolution of MEG to disambiguate the sources of the semantic interference and facilitation effects, which have critically shaped our understanding of how words are accessed in naming and reading. Our behavioral results replicated



the interference effect in naming and the facilitation effect in reading. Specifically, the fact that semantic relatedness delays naming times has led to the hypothesis that in object naming, semantically related words compete during lexical access. Here, we found mixed support for this hypothesis. Our comparison of naming and reading revealed that while the semantic facilitatory effect of word reading localized in the left STG in a time window consistent with lexical access, the interfering effect of object naming revealed a more complicated pattern. In fact, we observed a facilitation effect at 310–390 ms in the angular gyrus and posterior part of the STG, closely followed by a pattern consistent with interference at 395–485 ms in the anterior STG. Our speech-locked analysis also revealed two later effects of interference between 400–100 ms prior to word production, which is in line with motor preparatory accounts of interference. Importantly, we did not find any interference effects occurring earlier than the facilitation effect. In what follows we discuss the theoretical consequences and empirical limitations of these findings.

#### **Facilitation in Word Reading at 180–335 ms in Left Superior Temporal Cortex**

A classic semantic priming effect exhibits a reduction of MEG signal amplitude as a function of semantic similarity between prime and target. Thus, in our overt reading task, we expected facilitation to manifest as lower amplitudes for the semantically related versus the unrelated condition, followed by the lowest amplitudes for the identical condition, which involves repetition of the same word. Exactly this pattern was observed in the left superior temporal cortex at 180–335 ms, which is consistent with the localization of lexical access both in space (Hickok & Poeppel, 2007; Hillis, Rorden, & Fridriksson, 2017; Lau, Phillips, & Poeppel, 2008) and time (Bentin et al., 1985; Indefrey & Levelt, 2004). Thus, this effect has a straightforward interpretation in terms of spreading activation between semantically related lexical representations. Research on reading aloud has also shown connections between the STG and other areas relevant for semantic processing, such as the angular gyrus and the inferior temporal sulcus, forming a broader semantic network for reading aloud (Boukrina & Graves, 2013).

#### **Early Facilitation and Late Interference Patterns Characterize the Behavioral Interference Effect**

In contrast to word reading, our MEG data for object naming revealed a less straightforward pattern. In the stimulus-locked analysis, we observed an early facilitation effect followed by a later interference effect. The early facilitation effect was associated with decreased activation in the angular gyrus and posterior STG for the identical and semantically related primes as compared with the unrelated primes, but no distinction between the identical and semantically related primes emerged. The angular gyrus has been associated with the semantic system and specifically with conceptual retrieval and conceptual integration (Binder, Desai, Graves, & Conant, 2009), as well as with decreased activity for cross-modal priming effects (Badgaiyan, Schacter, & Alpert, 1999). As previously mentioned, the STG has been associated with lexical access (Hickok & Poeppel, 2007; Hillis et al., 2017; Lau et al., 2008). Further, while the early effect showed a pattern where both the semantically related and identical conditions separated in the same direction from the unrelated condition, the late effect patterned such that the semantically related and identical conditions separated in opposite direction from the unrelated condition. That is, the facilitation-eliciting identical priming showed an increase in activation relative to the unrelated condition, while the interfering semantic primes showed the opposite pattern: a decrease in activation compared with the unrelated condition. This pattern is consistent with similarity-based interference between related but not identical



meanings and is inversely related to the behavioral RTs, meaning that as activation at the interference cluster increased, RTs decreased.

Crucially, the time resolution of our measurement allowed us to determine whether a possible interference pattern occurs early, during conceptual preparation or lexical access, or at later, postlexical stages of processing. The stimulus-locked results conformed to the latter hypothesis, showing first a facilitation at 310–390 ms in the angular gyrus and posterior part of the STG, possibly representing lexical-level processes, followed by a later interference pattern at 395–485 ms. Our scaled estimates of the underlying processes occurring during the 395–485 ms time window suggest that the later interference effect occurs during phonological code retrieval. In addition, the interference effect localized in the anterior parts of the STG and the insular cortex. Further, the presence of an early facilitatory effect is in line with competitive accounts of lexical access that describe a phenomenon of reverse priming that is associated with the semantic interference effect (Piai et al., 2014; Roelofs, Piai, Rodriguez, & Chwilla, 2016), although it is also predicted by the REH (Janssen et al., 2008). While it is not possible to determine the exact underlying processes associated with the later interference cluster, the late timing of the cluster as well as the fact that it occurs after the facilitation effect suggests that it is too late to reflect lexical or prelexical stages of processing. Further, the activity in the insular cortex cannot be confidently interpreted since the localization of deep sources with MEG is still controversial (Krishnaswamy et al., 2017).

The response-locked analysis revealed two different effects. The first effect was observed at –200 ms to –100 ms prior to naming time and localized at the anterior part of the intraparietal sulcus. This extremely late effect is estimated to occur during the very last stages of object naming, when the motor response is being planned. This is exactly in line with the response exclusion hypothesis, which postulates that the semantic interference effect occurs as a result of a decision that has to be made at the articulators. A core principle of the REH is that words receive privileged access to the motor preparation system over images. As a result, the primes must be excluded from the single-channel motor preparation buffer before the target image can be named. Still, the mechanism by which the response buffer excludes responses according to the REH is still not fully specified. For instance, more details regarding the mechanism of the decision process at the buffer are required. It is worth mentioning that the spatial localization of the late effect that we found does not occur in frontal areas such as the premotor and motor cortices, which are usually associated with phonetic encoding and articulatory plans (Indefrey, 2011).

In contrast to this late result, the second response-locked analysis revealed a second, more sustained effect in the posterior part of the parahippocampal gyrus starting at –400 ms until –100 ms, with the semantically related condition peaking at –200 ms before utterance time. After scaling the timing of this cluster to be proportional to the RTs that we observed, the effect appears to start during lexical access stages and to sustain until motor preparation.

As opposed to the facilitation effect in reading, which localized at a single time window, the results for the object naming task revealed that the semantic interference has multiple loci. The semantic interference effect seems to be characterized by an early facilitation, possibly at the lexical level, followed by two focal interference effects at the phonological retrieval and motor preparation stages. The interference also appeared as a sustained effect starting at the lexical level until motor preparation. Previous literature has shown variable timings for the localization of semantic interference findings, with some effects pointing to an early, lexical stage of processing (Aristei et al., 2011; Maess et al., 2002; Piai et al., 2014; Roelofs, 2018), while other findings support a postlexical locus (Anders et al., 2019; Blackford et al., 2012; Janssen et al., 2014). Evidence for both an early and a late locus of interference have also been

found in a blocked semantic interference paradigm using intracranial EEG with eight epileptic patients (Anders et al., 2019) where the authors found increased activity in the presupplementary motor area at 200–300 ms and at 700–800 ms, which was interpreted, respectively, as an initial conflict resolution and as prereponse control processes. One possibility for the inconsistencies in the literature might come from variabilities in paradigms and neuroimaging methods. Nevertheless, some findings point for a common lexical level locus for semantic interference, which appears across many variations of the classical picture-word interference paradigm when proportional scaling is done to account for RTs (Roelofs & Shitova, 2017). However, some findings, including what is presented here, still found very late effects that seem to be postlexical even after scaling (Janssen et al., 2014). If the effect indeed has multiple loci, then it is possible that variations in the experimental paradigms and in the neuroimaging methods might bias one of the loci of the interference effect to be picked up in some cases but not others. What we show here is that indeed, the semantic interference effect has a complex neural signature, consisting of both early and late effects. Specifically, the single early lexical-level effect that we found here revealed a facilitatory pattern, while the later effects all showed an interference pattern, including a very late motor-preparation effect.

#### **Priming Effects Constant across SOAs**

In both the omnibus and the within-task analyses of the MEG data, we found main effects of SOA, but surprisingly, no interaction of SOA with any other factors. Crucially, SOA did not interact with Prime Type in either the MEG or the behavioral data. We therefore conclude that on average our priming results generalize across all the SOAs that we tested. However, in the context of the current study, the effect of SOA is only meaningful if it interacts with the other factors, mainly Prime Type. Because the effect of SOA did not modulate that of Prime Type, we will not further discuss the implications of this factor. Note that there is evidence showing that SOA manipulation can change the size and even the direction of priming, specifically in Object Naming (Heij et al., 1990; Xavier et al., 2000), and it is likely that SOAs longer than 400 ms might interact with Prime Type and/or Task.

#### **Widespread Effect of Task**

We observed a widespread effect of Task that covered almost the entire left hemisphere, throughout the whole analysis time window, with the most reliable signal centered at medial occipital areas. This large effect might be driven not only by the contrasting tasks, but also by the contrasting modalities of the primes. In fact, in Word Reading, the prime and the target are both written words, whereas in Object Naming, the prime is a word while the target is an image. Therefore, our widespread effect could have been driven by the tasks themselves, or by matching vs. mismatching modalities of the prime and target. We speculate that the effect was likely driven by both of these contrasts, given its extensive coverage in both time and space.

#### **Limitations and Future Directions**

It is worth mentioning that one of the challenges in trying to answer the question of early vs. late effects is in objectively defining what is late and what is early. Models of word production lay out processing steps differently, the main distinction being serial vs. parallel models (Hickok, 2012; Price, 2012). Here our findings are compared to estimated timings from the serial model of Indefrey and Levelt (2004), which has received support but has also been criticized for not being backed enough by neural data to justify the pure seriality of the model

(Strijkers & Costa, 2011, 2016). For instance, there is MEG evidence of semantic and phonological information beginning in parallel as early as 100–250 ms after picture onset (Blanco-Elorrieta, Ferreira, Del Prato, & Pykkänen, 2018; Miozzo, Pulvermüller, & Hauk, 2014; Pulvermüller, Shtyrov, & Hauk, 2009). Furthermore, other top-down processes, such as feedback, have to be taken into consideration to properly make a one-to-one match between the neural data and the models of word production (Strijkers & Costa, 2016). Nevertheless, lexical access has been supported consistently to occur about 200 ms after stimulus onset (Strijkers & Costa, 2011), and the debate regarding the extent of seriality and parallelism of word production is still open. Here we lay out the estimated spatiotemporal signature of the semantic interference effect based on what is currently known of the processing stages of both reading and naming, based on a well-established model. As models of naming and reading are further developed and a consensus regarding the seriality or parallelism of processing is reached, the understanding of electrophysiological results will hopefully also improve.

### Conclusion

We used MEG to provide a spatiotemporal characterization of the neural signatures associated with two well-established behavioral effects during lexical processing: semantic interference in object naming and semantic facilitation in overt reading. While the facilitation in reading was characterized only by an early lexical-level effect in the STG, the behavioral interference effect came with a more complex neural pattern. It consisted of both an early facilitatory effect in the angular gyrus, estimated to occur during lexical processing, and a later, sustained interference effect in multiple regions, likely occurring during both phonological retrieval and motor preparation. These results suggest that the semantic interference effect in naming is a multi-locus effect, which may explain the discrepancies in prior literature regarding whether it occurs at the early lexical level, or at a later postlexical level.

### FUNDING INFORMATION

Liina Pykkänen, NYUAD Research Institute, Award ID: G1001.

### AUTHOR CONTRIBUTIONS

Both Julien Dirani and Liina Pykkänen designed the research and wrote the paper. Julien Dirani performed the research and analyzed the data.

### 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*(1), 669–672.
- Anders, R., Llorens, A., Dubarry, A.-S., Trébuchon, A., Liégeois-Chauvel, C., & Alario, F.-X. (2019). Cortical dynamics of semantic priming and interference during word production: An intracerebral study. *Journal of Cognitive Neuroscience*, *31*(7), 978–1001. [http://doi.org/10.1162/jocn\\_a\\_01406](http://doi.org/10.1162/jocn_a_01406)
- Aristei, S., Melinger, A., & Abdel Rahman, R. (2011). Electrophysiological chronometry of semantic context effects in language production. *Journal of Cognitive Neuroscience*, *23*(7), 1567–1586.
- Badgaiyan, R. D., Schacter, D. L., & Alpert, N. M. (1999). Auditory priming within and across modalities: Evidence from positron emission tomography. *Journal of Cognitive Neuroscience*, *11*(4), 337–348.
- Bentin, S., McCarthy, G., & Wood, C. C. (1985). Event-related potentials, lexical decision and semantic priming. *Electroencephalography and Clinical Neurophysiology*, *60*(4), 343–355.
- 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.
- Blackford, T., Holcomb, P. J., Grainger, J., & Kuperberg, G. R. (2012). A funny thing happened on the way to articulation: N400 attenuation despite behavioral interference in picture naming. *Cognition*, *123*(1), 84–99.
- Blanco-Elorrieta, E., Ferreira, V. S., Del Prato, P., & Pykkänen, L. (2018). The priming of basic combinatory responses in MEG. *Cognition*, *170*, 49–63.

- Bloem, I., & La Heij, W. (2003). Semantic facilitation and semantic interference in word translation: Implications for models of lexical access in language production. *Journal of Memory and Language*, 48(3), 468–488.
- Bloem, I., van den Boogaard, S., & La Heij, W. (2004). Semantic facilitation and semantic interference in language production: Further evidence for the conceptual selection model of lexical access. *Journal of Memory and Language*, 51(2), 307–323.
- Boukrina, O., & Graves, W. W. (2013). Neural networks underlying contributions from semantics in reading aloud. *Frontiers in Human Neuroscience*, 7, 518.
- Brodbeck, C. (2017). Eelbrain (Version v0.25). Zenodo. <http://doi.org/10.5281/zenodo.438193>
- Costa, A., Alario, F.-X., & Caramazza, A. (2005). On the categorical nature of the semantic interference effect in the picture-word interference paradigm. *Psychonomic Bulletin & Review*, 12(1), 125–131.
- Dale, A. M., Liu, A. K., Fischl, B. R., Buckner, R. L., Belliveau, J. W., Lewine, J. D., & Halgren, E. (2000). Dynamic statistical parametric mapping: Combining fMRI and MEG for high-resolution imaging of cortical activity. *Neuron*, 26(1), 55–67.
- de Zubicaray, G. I., Hansen, S., & McMahon, K. L. (2013). Differential processing of thematic and categorical conceptual relations in spoken word production. *Journal of Experimental Psychology: General*, 142(1), 131–142.
- de Zubicaray, G. I., Wilson, S. J., McMahon, K. L., & Muthiah, S. (2001). The semantic interference effect in the picture-word paradigm: An event-related fMRI study employing overt responses. *Human Brain Mapping*, 14(4), 218–227.
- Dhooge, E., & Hartsuiker, R. J. (2010). The distractor frequency effect in picture–word interference: Evidence for response exclusion. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 36(4), 878–891.
- Engemann, D. A., & Gramfort, A. (2015). Automated model selection in covariance estimation and spatial whitening of MEG and EEG signals. *NeuroImage*, 108, 328–342.
- Fieder, N., Wartenburger, I., & Rahman, R. A. (2019). A close call: Interference from semantic neighbourhood density and similarity in language production. *Memory & Cognition*, 47(1), 145–168.
- Finkbeiner, M., & Caramazza, A. (2006a). Lexical selection is not a competitive process: A reply to La Heij et al. (2006). *Cortex*, 42(7), 1032–1036.
- Finkbeiner, M., & Caramazza, A. (2006b). Now you see it, now you don't: On turning semantic interference into facilitation in a Stroop-like task. *Cortex*, 42(6), 790–796.
- Giesbrecht, F. G., & Burns, J. C. (1985). Two-stage analysis based on a mixed model: Large-sample asymptotic theory and small-sample simulation results. *Biometrics*, 477–486.
- Giezen, M. R., & Emmorey, K. (2016). Language co-activation and lexical selection in bimodal bilinguals: Evidence from picture–word interference. *Bilingualism: Language and Cognition*, 19(2), 264–276.
- Glaser, W. R., & Glaser, M. O. (1989). Context effects in stroop-like word and picture processing. *Journal of Experimental Psychology: General*, 118(1), 13–42.
- Gramfort, A., Luessi, M., Larson, E., Engemann, D. A., Strohmeier, D., Brodbeck, C., ... Hämäläinen, M. S. (2014). MNE software for processing MEG and EEG data. *NeuroImage*, 86, 446–460.
- Hala, S., Pexman, P. M., & Glenwright, M. (2007). Priming the meaning of homographs in typically developing children and children with autism. *Journal of Autism and Developmental Disorders*, 37(2), 329.
- Hickok, G. (2012). Computational neuroanatomy of speech production. *Nature Reviews Neuroscience*, 13(2), 135.
- Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, 8(5), 393.
- Hillis, A. E., Rorden, C., & Fridriksson, J. (2017). Brain regions essential for word comprehension: Drawing inferences from patients. *Annals of Neurology*, 81(6), 759–768.
- Holcomb, P. J. (1988). Automatic and attentional processing: An event-related brain potential analysis of semantic priming. *Brain and Language*, 35(1), 66–85.
- Holcomb, P. J., & Anderson, J. E. (1993). Cross-modal semantic priming: A time-course analysis using event-related brain potentials. *Language and Cognitive Processes*, 8(4), 379–411.
- Holmes, A. P., Blair, R., Watson, J., & Ford, I. (1996). Nonparametric analysis of statistic images from functional mapping experiments. *Journal of Cerebral Blood Flow & Metabolism*, 16(1), 7–22.
- Hong-Tai Fai, A., & Cornelius, P. L. (1996). Approximate F-tests of multiple degree of freedom hypotheses in generalized least squares analyses of unbalanced split-plot experiments. *Journal of Statistical Computation and Simulation*, 54(4), 363–378. <https://doi.org/10.1080/00949659608811740>
- Indefrey, P. (2011). The spatial and temporal signatures of word production components: A critical update. *Frontiers in Psychology*, 2(255). <https://doi.org/10.3389/fpsyg.2011.00255>
- Indefrey, P., & Levelt, W. J. (2004). The spatial and temporal signatures of word production components. *Cognition*, 92(1–2), 101–144.
- Janssen, N., Hernández-Cabrera, J. A., van der Meij, M., & Barber, H. A. (2014). Tracking the time course of competition during word production: Evidence for a post-retrieval mechanism of conflict resolution. *Cerebral Cortex*, 25(9), 2960–2969.
- Janssen, N., Schirm, W., Mahon, B. Z., & Caramazza, A. (2008). Semantic interference in a delayed naming task: Evidence for the response exclusion hypothesis. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 34(1), 249–256.
- Katz, L., & Feldman, L. B. (1983). Relation between pronunciation and recognition of printed words in deep and shallow orthographies. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 9(1), 157–166.
- 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.
- Krishnaswamy, P., Obregon-Henao, G., Ahveninen, J., Khan, S., Babadi, B., Iglesias, J. E., ... Purdon, P. L. (2017). Sparsity enables estimation of both subcortical and cortical activity from MEG and EEG. *Proceedings of the National Academy of Sciences*, 114(48), E10465–E10474.
- Kuznetsova, A., Brockhoff, P., & Christensen, R. (2017). lmerTest: Tests in linear mixed effects models. R package version 2.0–33. 2016. *Journal of Statistical Software*, 82(13), 1–26.
- La Heij, W. (1988). Components of Stroop-like interference in picture naming. *Memory & Cognition*, 16(5), 400–410.
- La Heij, W., Dirx, J., & Kramer, P. (1990). Categorical interference and associative priming in picture naming. *British Journal of Psychology*, 81(4), 511–525.
- Lau, E. F., Phillips, C., & Poeppel, D. (2008). A cortical network for semantics: (De)constructing the N400. *Nature Reviews Neuroscience*, 9(12), 920–933.
- Levelt, W. J. (2001). Spoken word production: A theory of lexical access. *Proceedings of the National Academy of Sciences*, 98(23), 13464–13471.



- Levelt, W. J., Roelofs, A., & Meyer, A. S. (1999). A theory of lexical access in speech production. *Behavioral and Brain Sciences*, 22(1), 1–38.
- Lupker, S. J. (1979). The semantic nature of response competition in the picture-word interference task. *Memory & Cognition*, 7(6), 485–495.
- Maess, B., Friederici, A. D., Damian, M., Meyer, A. S., & Levelt, W. J. (2002). Semantic category interference in overt picture naming: Sharpening current density localization by PCA. *Journal of Cognitive Neuroscience*, 14(3), 455–462.
- Mahon, B. Z., Costa, A., Peterson, R., Vargas, K. A., & Caramazza, A. (2007). Lexical selection is not by competition: A reinterpretation of semantic interference and facilitation effects in the picture-word interference paradigm. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 33(3), 503.
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, 164(1), 177–190.
- Matsumoto, A., Iidaka, T., Haneda, K., Okada, T., & Sadato, N. (2005). Linking semantic priming effect in functional MRI and event-related potentials. *NeuroImage*, 24(3), 624–634. <https://doi.org/10.1016/j.neuroimage.2004.09.008>
- Miozzo, M., Pulvermüller, F., & Hauk, O. (2014). Early parallel activation of semantics and phonology in picture naming: Evidence from a multiple linear regression MEG study. *Cerebral Cortex*, 25(10), 3343–3355.
- Munding, D., Dubarry, A.-S., & Alario, F.-X. (2016). On the cortical dynamics of word production: A review of the MEG evidence. *Language, Cognition and Neuroscience*, 31(4), 441–462.
- Peirce, J. W. (2007). PsychoPy—psychophysics software in Python. *Journal of Neuroscience Methods*, 162(1–2), 8–13.
- Piai, V., Roelofs, A., Jensen, O., Schoffelen, J.-M., & Bonnefond, M. (2014). Distinct patterns of brain activity characterise lexical activation and competition in spoken word production. *PLoS One*, 9(2), e88674.
- Price, C. J. (2012). A review and synthesis of the first 20 years of PET and fMRI studies of heard speech, spoken language and reading. *NeuroImage*, 62(2), 816–847.
- Pulvermüller, F., Shtyrov, Y., & Hauk, O. (2009). Understanding in an instant: Neurophysiological evidence for mechanistic language circuits in the brain. *Brain and Language*, 110(2), 81–94.
- R Core Team. (2013). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Riès, S., Janssen, N., Burle, B., & Alario, F.-X. (2013). Response-locked brain dynamics of word production. *PLoS One*, 8(3), e58197.
- Rissman, J., Eliassen, J. C., & Blumstein, S. E. (2003). An event-related fMRI investigation of implicit semantic priming. *Journal of Cognitive Neuroscience*, 15(8), 1160–1175.
- Roelofs, A. (2003). Goal-referenced selection of verbal action: Modeling attentional control in the Stroop task. *Psychological Review*, 110(1), 88–125.
- Roelofs, A. (2018). A unified computational account of cumulative semantic, semantic blocking, and semantic distractor effects in picture naming. *Cognition*, 172, 59–72.
- Roelofs, A., Piai, V., Rodriguez, G. G., & Chwilla, D. J. (2016). Electrophysiology of cross-language interference and facilitation in picture naming. *Cortex*, 76, 1–16.
- Roelofs, A., Piai, V., & Schriefers, H. (2011). Selective attention and distractor frequency in naming performance: Comment on Dhooge and Hartsuiker (2010). *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 37, 1032–1038.
- Roelofs, A., & Shitova, N. (2017). Importance of response time in assessing the cerebral dynamics of spoken word production: Comment on Munding et al. (2016). *Language, Cognition and Neuroscience*, 32(8), 1064–1067.
- Rose, S. B., Aristei, S., Melinger, A., & Abdel Rahman, R. (2019). The closer they are, the more they interfere: Semantic similarity of word distractors increases competition in language production. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 45(4), 753.
- 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.
- Rosson, M. B. (1983). From SOFA to LOUCH: Lexical contributions to pseudoword pronunciation. *Memory & Cognition*, 11(2), 152–160.
- Sailor, K., & Brooks, P. J. (2014). Do part-whole relations produce facilitation in the picture-word interference task? *The Quarterly Journal of Experimental Psychology*, 67(9), 1768–1785.
- Sailor, K., Brooks, P. J., Bruening, P. R., Seiger-Gardner, L., & Guterman, M. (2009). Exploring the time course of semantic interference and associative priming in the picture-word interference task. *Quarterly Journal of Experimental Psychology*, 62(4), 789–801.
- Starreveld, P. A., & La Heij, W. (1995). Semantic interference, orthographic facilitation, and their interaction in naming tasks. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 21(3), 686.
- Strijkers, K., & Costa, A. (2011). Riding the lexical speedway: A critical review on the time course of lexical selection in speech production. *Frontiers in Psychology*, 2, 356.
- Strijkers, K., & Costa, A. (2016). The cortical dynamics of speaking: Present shortcomings and future avenues. *Language, Cognition and Neuroscience*, 31(4), 484–503.
- Van Essen, D. C. (2005). A population-average, landmark- and surface-based (PALS) atlas of human cerebral cortex. *NeuroImage*, 28(3), 635–662.
- Vinogradov, S., Ober, B. A., & Shenaut, G. K. (1992). Semantic priming of word pronunciation and lexical decision in schizophrenia. *Schizophrenia Research*, 8(2), 171–181.
- Xavier, A., Segui, J., & Ferrand, L. (2000). Semantic and associative priming in picture naming. *The Quarterly Journal of Experimental Psychology: Section A*, 53(3), 741–764.