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Top-down resolution of lexico-semantic competition in speech production and the role of the left inferior frontal gyrus: an fMRI study

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ABSTRACT

Recent neurobiological speech production accounts propose the left inferior frontal gyrus (LIFG) resolves lexical competition using top-down control. The current fMRI experiment investigates whether response set membership influences LIFG involvement. In the picture-word interference paradigm target pictures were presented with distractor words that were, or were not, targets on other trials. Production models predict greater LIFG involvement in the high-coactivation trials with response set target-distractor pairs. Surprisingly, we found no effect of response set. Semantic interference elicited activation in the left posterior temporal cortex, similar to previous reports. Pooling data across response set conditions revealed additional significant activation in pars orbitalis of the LIFG, indicating detection benefited from the additional statistical power. Our findings challenge the co-activation assumption and indicate inconsistent LIFG results reported in the literature might reflect a combination of small effect size and low signal-to-noise, thus questioning the prominent role afforded to the LIFG.

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1. Introduction

Speech production processes are affected by context. For instance, picture naming latencies increase in the context of naming items from the same semantic category compared to unrelated items (e.g. Abdel Rahman & Melinger, 2007; Belke, 2008; Belke et al., 2005; Blaxton & Neely, 1983; Brown, 1981; Damian et al., 2001; Damian & Als, 2005; Howard et al., 2006; Hsiao et al., 2009; Kroll & Stewart, 1994; Schnur et al., 2006; Vigliocco et al., 2002; Wheeldon & Monsell, 1994). This effect is known as semantic interference, and is reliably observed across a range of experimental naming paradigms.


1.1. Psycholinguistic and neurolinguistic models of lexical access

Models of lexical access in spoken word production assume that context items from the same semantic category co-activate each other either at the conceptual (Dell'Acqua et al., 2007; van Maanen et al., 2009) or conceptual-to-lexical level (e.g. Belke, 2013; Howard et al., 2006; Oppenheim et al., 2010), with activation then

spreading to lexical and post-lexical levels. According to lexical-selection-by-competition accounts, the increased activation of multiple categorically related candidates delays the selection process at the lexical level (e.g. Roelofs, 1992). Alternative non-competitive selection accounts assume lexical retrieval depends solely on the activation level of the target representation and is accomplished after a specified number of time steps or when activation exceeds a predetermined threshold (e.g. Caramazza, 1997; Dell & O'Seaghda, 1992). Some accounts additionally assume a prominent role for domain general cognitive control, acting as a top-down, selection-biasing or activation-boosting mechanism whose purpose is to assist selection among activated lexical candidates (e.g. Belke & Stielow, 2013; Oppenheim et al., 2010; Schnur et al., 2009). However, some explanations for semantic interference vary according to the nature of the naming paradigm, as we will explain in more detail below.

Neurobiological accounts of production implicate a network of left-hemisphere regions in lexico-semantic interference. The left middle (MTG) and superior temporal gyrii (pSTG) are proposed to play important roles

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in lexical-semantic processes such as lemma selection and phonological word form retrieval (e.g. Indefrey, 2011; Indefrey & Levelt, 2004). Accordingly, fMRI studies of semantic interference across various naming paradigms consistently report a reduced response in the mid-to-posterior MTG/STG associated with semantic interference (for a review, see de Zubicaray & Piai, 2019). The role of the MTG in processing semantic information is further supported by a number of patient studies (e.g. Baldo et al., 2013; Harvey & Schnur, 2015; Piai & Knight, 2018; Schwartz et al., 2009; Walker et al., 2011).

Some accounts additionally assume a prominent role for the left inferior frontal gyrus (LIFG) in implementing domain general cognitive control (e.g. Belke & Stielow, 2013; Oppenheim et al., 2010; Schnur et al., 2009). In particular, the LIFG is proposed to be essential for enhancing or modulating lexical activation to resolve conflict between multiple response options (Heim et al., 2009; Oppenheim et al., 2010; Roelofs, 2018; Schnur et al., 2009; Thompson-Schill et al., 1997; Thompson-Schill et al., 1998; Thompson-Schill et al., 1999). For example, Belke and Stielow (2013) proposed that “any future model of word production unavoidably faces the challenge of specifying how left frontal mechanisms of domain-general cognitive control interact with paradigmatic interference during lexical-semantic encoding” (p. 23). Thus, according to these accounts, if semantic interference in naming arises from multiple lexical candidates being activated, then we should reliably observe LIFG involvement associated with it. However, across the various naming paradigms that evoke semantic interference, LIFG involvement has not been reliably observed (see de Zubicaray & Piai, 2019). A closer look at the literature indicates that such inconsistency might be explained by key methodological differences between the studies, which we will examine in the next section.

1.2. Cerebral regions associated with semantic interference across different naming paradigms

In the continuous naming paradigm, participants name multiple exemplars from a semantic category at different ordinal positions or *lags* with unrelated pictures in intervening trials (Howard et al., 2006). A cumulative semantic interference is observed over consecutive presentations: as each additional item is named from the semantic category, naming latencies increase linearly by ~30 ms. All production accounts attribute semantic interference in this paradigm to activation of multiple lexical candidates, resolved by either competitive (Belke, 2013; Roelofs, 2018) or non-competitive

(Oppenheim et al., 2010) lexical selection mechanisms, with some accounts also implicating the LIFG in top-down enhancement of lexical activation (Oppenheim et al., 2010; Roelofs, 2018; but see Belke, 2013). Interestingly, LIFG lesions do not influence semantic interference in this task (Riès et al., 2015), and differential LIFG activity is not observed in EEG studies in healthy participants (e.g. Costa et al., 2009; Rose & Rahman, 2016), and inconsistently across two fMRI studies (e.g. Canini et al., 2016; cf. de Zubicaray et al., 2015).

In the blocked cyclic naming paradigm, participants name repeating cycles of sets (e.g. 4–6 items) of categorically related (homogeneous) and unrelated (heterogeneous) pictures in an alternating fashion. From the second cycle onwards semantic interference is observed: items are named slower in homogenous compared to heterogeneous blocks (Damian et al., 2001; Damian & Als, 2005; Kroll & Stewart, 1994). Both competitive (Belke, 2013; Roelofs, 2018) and non-competitive (Oppenheim et al., 2010) lexical selection accounts, respectively, have also implicated the LIFG in top-down enhancement of lexical activation in this paradigm. Neuroimaging and lesion studies provide consistent evidence for left pMTG/STG engagement and relatively less consistent evidence for LIFG involvement during semantic interference in blocked cyclic naming (e.g. Biegler et al., 2008; de Zubicaray et al., 2014; Harvey & Schnur, 2015; Maess et al., 2002; Python et al., 2018; Schnur et al., 2005, 2006, 2009. See Meinzer et al., 2016, for an overview).

In the picture-word interference (PWI) paradigm, participants name pictures while ignoring a distractor word. When the distractor word is categorically related to the target picture, naming latencies are slower compared to unrelated distractors. Lexical-selection-by-competition accounts attribute this semantic interference effect to the related distractor and target concepts priming each other, increasing the activation levels of their lexical representations, thus making the selection of the target’s lexical representation more time-consuming (Roelofs, 1992, 2018). Post-lexical accounts assume the increase in activation at the conceptual or conceptual-to-lexical level results in semantic priming, whereas the locus of interference is in an articulatory output buffer where a top-down decision mechanism acts to outweigh the priming effect using task-relevant criteria such as semantic category information (Dhooge & Hartsuiker, 2011; Finkbeiner & Caramazza, 2006; Mahon et al., 2007). Recent lexical-selection-by-competition accounts also implicate the LIFG in top-down enhancement of lexical activation in PWI (Roelofs, 2018), and Indefrey’s (2011) meta-analysis implicated the LIFG in phonetic encoding, where articulatory

programmes are encoded and buffered, making it a plausible candidate for the locus of interference in the post-lexical account. Neuroimaging studies investigating the neural correlates of semantic interference in the PWI task have reliably observed pMTG/STG activation *decreases* (de Zubicaray et al., 2013; Piai et al., 2013, 2014), and occasionally LIFG involvement (Abel et al., 2009, 2012; de Zubicaray et al., 2009). Patients with lesions to the LIFG fail to show differential semantic interference in PWI (Piai et al., 2016; Piai & Knight, 2018).

As the BOLD signal reductions in pMTG/STG observed reliably across PWI fMRI studies are due to a contrast of related versus unrelated conditions in the presence of an implicit global baseline specific to each experiment, they can be attributed to a relatively lower signal in one condition compared to the other. This occurs in the context of pre-experimental familiarisation with the target pictures and balanced item repetition in both conditions. It is well known that repeated items demonstrate reduced BOLD signal relative to novel items (i.e. repetition suppression; Grill-Spector et al., 2006). However, as intracranial electrophysiological studies have shown, BOLD signal reductions do not always correspond to reduced neuronal activation in terms of either local field potentials (LFPs) or spike rates (Ekstrom, 2010), complicating interpretation. If a strong assumption of coupled neuronal-BOLD activation is made, then a signal decrease for the related condition might reflect either of two possible mechanisms proposed by different production accounts based upon spreading activation. For example, it might reflect lateral inhibition of semantic competitors, the purpose of which is to suppress mismatching information at the lexical level in selection-by-competition models (e.g. Berg & Schade, 1992; Harley, 1993; see de Zubicaray & McMahon, 2009). Alternatively, the BOLD signal reductions observed in the MTG might represent semantic priming as the response exclusion hypothesis proposes (Mahon et al., 2007).

Although semantic interference is observed across all of these naming paradigms, the paradigms vary with respect to a key design feature: *response set membership*. Could this feature explain the lack of consistent LIFG findings across studies? Response set membership refers to target pictures that are also context items in the same experiment. In the continuous naming paradigm, none of the items are response set members. Conversely, in the blocked cyclic naming paradigm in which LIFG involvement has been reported more frequently, all items are response set members and repeatedly presented. In the PWI paradigm, targets may or may not be response set members. According to lexical-selection-by-competition models such as WEAVER++, response set membership serves to increase the level

of co-activation between targets and distractors via repetition and reciprocal priming, resulting in greater competition (e.g. Piai et al., 2012; Roelofs, 1992, 2003, 2018). Semantic interference in the absence of response set membership is assumed to be weaker, reflecting indirect activation of competitors via mediated priming (e.g. Roelofs, 1992; cf. Caramazza & Costa, 2000). This raises the possibility that LIFG might intervene to resolve lexico-semantic competition as a function of the strength of co-activation among competing lexical candidates, with top down enhancement provided until selection occurs (Roelofs, 2018). According to the non-competitive post lexical account, increased lexical-conceptual co-activation should result in stronger semantic priming, which is proposed to *reduce* the magnitude of the interference effect accordingly (Mahon et al., 2007; but see Gauvin et al., 2018). If so, then LIFG should demonstrate differential activity during semantic interference in naming when response set membership is manipulated. Intriguingly, prior PWI studies have shown a pattern of significant LIFG activity for non-response set member distractor-target pairings (e.g. Abel et al., 2009, 2012; de Zubicaray et al., 2001) but not for response set membership (e.g. de Zubicaray et al., 2013; Piai et al., 2013).

In the current experiment, we tested whether LIFG involvement in lexico-semantic competition is a function of the level of distractor-target co-activation in the PWI task by manipulating response set membership (e.g. Piai et al., 2012; Roelofs, 1992). We hypothesised response set member target-distractor pairs would differentially activate the LIFG compared to non-response set pairs as predicted by both lexical-selection-by-competition and non-competitive post-lexical accounts (e.g. Abel et al., 2009, 2012; de Zubicaray & McMahon, 2009). Additionally, we expected this pattern to be paralleled in the left MTG/STG where neurobiological accounts assume lexico-semantic retrieval to occur (e.g. Indefrey, 2011; Roelofs, 2018) and previous studies of semantic interference in PWI have consistently demonstrated significant activity (e.g. de Zubicaray et al., 2013; Piai et al., 2013).

2 Materials and methods

2.1. Participants

Twenty participants (mean age 24, range 18-37, 14 female) were recruited from the University of Queensland. All were right-handed and native English speakers, with no history of neurological or psychiatric disorder, substance dependence, or known hearing deficits. All had normal or corrected-to-normal vision and gave

informed consent. The study was approved by the Royal Brisbane and Women's Hospital Human Research Ethics Committee (EC00172). Participants were reimbursed AUD \$30 for participating. Three additional participants were recruited, but their data was excluded due to technical malfunction (1) or incidental findings on their scans (2).

2.2. Task design

A 2 × 2 design was used with distractor type (Related vs. Unrelated) and response set membership (Response set member vs. Non-response set member) as within-participants factors.

2.3. Materials

Forty target pictures comprising five object exemplars from each of eight semantic categories (fruit, furniture, vehicles, animals, buildings, musical instruments, weapons, clothing). Each target picture was presented four times during the experiment, each time with a different distractor word. Half of the distractor words were target words on other trials, i.e. response set members. The distractor words in the related conditions were paired with different pictures to create identically matched unrelated distractors (see Appendix for a list of stimuli). Each target picture was thus paired with a semantically related response set distractor word (e.g. CAR-helicopter), a semantically related non-response set distractor word (CAR-truck), a semantically unrelated response set distractor word (CAR-bed) and a semantically unrelated non-response set distractor word (CAR-sofa). Pictures were selected from the Multipic normative database and had high name agreement (mean agreement 92%, SD 13%) (Duñabeitia et al., 2017). Distractors across response set conditions were matched closely (all $ps > .05$) on a range of lexical properties using the English

Lexicon Project and Glasgow normative databases (Balota et al., 2007; Scott et al., 2019), including log frequency (SUBTLEX; Brysbaert et al., 2013), the number of letters, phonemes, and syllables, orthographic Levenshtein distance (OLD), word mean bigram frequency, familiarity (Scott et al., 2019), concreteness, age of acquisition (Kuperman et al., 2012) and semantic diversity (Hoffman et al., 2013) (see Table 1).

Distractors appeared concurrent with the target picture (SOA=0) in Arial font, size 50, in red print and in capital letters. The location of the distractor varied randomly either above or below the picture. Trial presentation was pseudorandomised across participants using Mix software (van Casteren & Davis, 2006). Twenty different pseudorandomised lists were created, such that two presentations of the same picture were always interceded by at least five different pictures, no more than 2 consecutive trials were of the same distractor condition and consecutive trials had a different word onset. Each list was administered to 1 participant.

2.4. Apparatus

The Cogent 2000 toolbox extension (http://www.vislab.ucl.ac.uk/cogent_2000.php) for MATLAB (R2015b, Math Works, Inc.) was used for stimulus presentation, and presented via a personal computer onto a projector screen positioned at the rear of MRI system. Participants viewed the projected stimuli via a mirror attached to the head-coil, at approximately a 10° visual angle when positioned for scanning. Response recording was accomplished via a MR-compatible fibre-optic dual-channel noise-cancelling microphone attached to the head coil (FOMRI- III, Optoacoustics Ltd., Or-Yehuda, Israel; <http://www.optoacoustics.com>). Sound files were recorded by Cogent 2000 and post-experiment checked in Praat software version 6.0.21 (www.praat.org) for accuracy. RTs were determined automatically using Chronset software (Roux et al., 2017).

2.5. Procedure

Before entering the scanner room, the participant completed a familiarisation phase. During familiarisation, the participant was presented with the target pictures over three blocks. Within blocks, presentation order was randomised. During the first block, participants were presented with the target pictures and appropriate label printed below. During the following two blocks, only target pictures were presented. Participants were instructed to name the pictures as fast and accurately as possible throughout the three blocks. Erroneous responses were corrected by the experimenter.

Table 1. Lexical properties of the response set and non-response set distractors employed in the Experiment.

| Lexical Property | Distractor Type | | | |
|--------------------|-----------------|-----------|------------------|-----------|
| | Response set | | Non-response set | |
| | <i>M</i> | <i>SD</i> | <i>M</i> | <i>SD</i> |
| Letters | 5.15 | 1.86 | 5.2 | 1.44 |
| Phonemes | 4.08 | 1.58 | 4.3 | 1.18 |
| Syllables | 1.48 | 0.75 | 1.53 | 0.55 |
| OLD | 1.90 | 0.88 | 1.88 | 0.54 |
| Bigram Mean | 1732.19 | 676.12 | 1655.84 | 664.90 |
| Frequency | 3.04 | 0.58 | 2.86 | 0.48 |
| Familiarity | 5.92 | 0.68 | 5.73 | 0.72 |
| Concreteness | 4.88 | 0.11 | 4.87 | 0.11 |
| Age of Acquisition | 4.99 | 1.44 | 5.37 | 1.94 |
| Semantic Diversity | 1.49 | 0.19 | 1.47 | 0.24 |

Note: OLD = Orthographic Levenshtein Distance. SD = standard deviation. Refer to text for normative data sources.

The experimental session consisted of two blocks of 80 trials in which the 40 target items were presented in the four distractor conditions in pseudorandom order: semantically related response set, semantically related non-response set, unrelated response set and unrelated non-response set (160 trials in total). Each trial started with a 500 ms crosshair fixation point in the centre of the screen, followed by a 750 ms presentation of the target picture (10 × 10 cm) in the centre of the screen and the simultaneous presentation of the distractor word (SOA 0 ms). An intertrial interval (ITI) of 15 s was applied to accommodate the fMRI acquisition protocol. RTs were measured from onset of the target picture until the vocal response.

2.6. Image acquisition

Images were acquired using a 3 T Siemens MAGNETOM Prisma (Siemens Medical Systems, Erlangen, Germany) with a 64-channel head coil. A double gradient echo sequence with TR=520 ms, TE1 = 4.92, TE2 = 7.38 ms and isotropic voxel resolution of 3mm³ and a 60° flip angle was acquired to map b0 field inhomogeneity prior to acquiring the fMRI timeseries data. 162 BOLD gradient-echo EPI volumes were acquired across 2 equal consecutive sessions (40 slices, TA 3s, TR 14000 ms, TE 26 ms, 64 × 64 matrix, 3 mm × 3 mm in-plane resolution, 3 mm slice and a 90° flip angle). Per run 81 volumes were acquired, from which the first volume per run was discarded. Behavioural trials were interleaved with image acquisition using a sparse temporal sampling design (Gracco et al., 2005), which allows overt verbal responses to be made during a scanner off-phase to avoid articulation-related artifacts. At the start of each trial, no field gradients were

applied for a 4 s period of relative silence allowing for stimuli to be presented and recording of the participant's overt verbal response, then immediately applied for image acquisition. A single image volume was then acquired within 3 s, approximately coincident with the picture naming trial's estimated peak BOLD response. No field gradients were applied for an additional 8-s period to allow the BOLD response to the gradient noise to return to baseline (for a diagram of the imaging protocol, see Figure 1 of de Zubicaray et al., 2001). A 3D T1-weighted structural image was acquired with an MPRAGE sequence (1 mm isotropic voxel).

2.7. Data analysis

fMRI data were analysed using statistical parametric mapping software (SPM12; Wellcome Department of Imaging Neuroscience, Queen Square, London, U.K.). The first image of each fMRI series was discarded. The remaining images were realigned to the first image of the first series using the "Realign and Unwarp" function. From the realigned series a mean image was generated and coregistered to the T1-weighted image. Using the "Segment" procedure, the T1 weighted image was segmented. The "DARTEL" toolbox (Ashburner, 2007) was used to create a custom group template from the segmented grey and white matter images. Individual flow fields were then used to normalise the realigned fMRI volumes to the Montreal Neurological Institute (MNI) atlas T1 template. The images were resampled to 2 × 2 × 2 mm isotropic voxels and smoothed with a 8-mm FWHM isotropic Gaussian kernel. Estimation and removal of global signal effects was accomplished using a voxel level linear model (Macey et al., 2004). Finally, the images from each distractor condition were

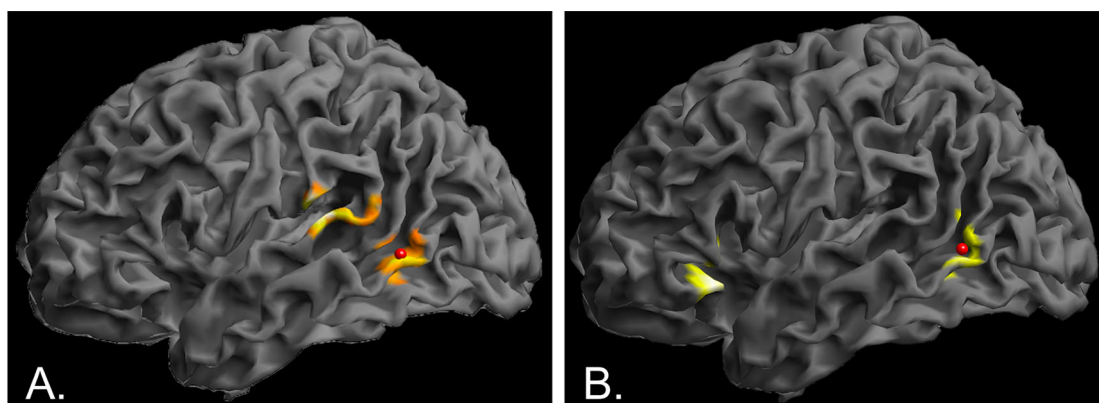


Figure 1. Semantic interference (Related > Unrelated), left hemisphere surface rendering of the response set membership condition with significant activation clusters in the posterior STG and MTG (panel A, left), and across combined items (Response set + Non-response set distractors) with significant activation clusters in the left IFG and pMTG (panel B, right). Whole brain maps were thresholded at $p < .005$ (uncorrected) for visualisation purposes. pMTG peaks are highlighted with a red dot.

Table 2. Peak maxima taken from previous fMRI studies used for confirmatory small volume corrections (SVCs).

| Study | Peak maxima (MNI space) | Cerebral region |
|---------------------------------|-------------------------|-----------------|
| de Zubicaray et al. (2013) | -54, -9, -15 | left mid-MTG |
| | -57, -57, -3 | left pMTG |
| de Zubicaray and McMahon (2009) | -54, -18, 0 | left mid-MTG |
| | -609, -30, 3 | left pMTG/STG |
| | -51, 24, -9 -48, 21, 18 | left IFG |
| | | left IFG |
| Piai et al. (2013) | -48, 4, 0 | left mid-STG |
| Abel et al. (2012) | -48, -34, 13 | left pSTG |
| | -30, 29, -1 | left IFG |

Key: MTG = middle temporal gyrus, STG = superior temporal gyrus, p = posterior, left IFG = left inferior frontal gyrus

regrouped to comprise a single epoch and errors assigned to a separate condition.

A two-stage, mixed effects statistical analysis was conducted. Epoch types corresponding to the four distractor-types and an error condition were modelled as effects of interest with delta functions representing each picture onset, and convolved with a basis function consisting of a single finite impulse response (FIR) with a window length corresponding to the epoch length. Trials were not convolved with a conventional hemodynamic response function, as the sparse image sequence does not acquire BOLD time course information (see Eden et al., 1999; Elliott et al., 1999; Gracco et al., 2005). Linear contrasts were applied to each participant's parameter estimates at the fixed effects level, then entered in a group level random effects repeated measures ANOVA in which covariance components were estimated using a restricted maximum likelihood (REML) procedure to correct for non-sphericity (Friston et al., 2002).

As we had a priori hypotheses implicating specific temporal and frontal brain regions involved in semantic interference in PWI, we predefined regions of interest (ROI) for analysis via small volume corrections (SVC) for 10-mm radius spheres centred on peaks in MNI space reported by previous fMRI PWI studies that used identical contrasts (i.e. categorically related vs unrelated; see Table 2).

We also adopted the following ROI maximum likelihood gray matter maps a priori from the Hammers et al. (2003) 3-D probabilistic atlas based on prior reports of peaks from PWI studies: left posterior superior temporal gyrus and left posterior temporal lobe, left middle and inferior temporal gyrus, left and right ACC (conflict monitoring/top-down control; e.g. de Zubicaray et al., 2001; Piai et al., 2013), and left inferior frontal gyrus. Note that by estimating SVC thresholds from all voxels within the larger anatomical ROIs, this approach produces a more conservative threshold for controlling type 1 error. An exploratory whole brain analysis was

conducted in addition to the ROI analyses with SVC. A height threshold of $p < .001$ was adopted in conjunction with a cluster FWE corrected threshold of $p < .05$ estimated for the whole brain and for each ROI.

3. Results

3.1. Behavioural data

The following trials were removed before data analysis: trials on which the voice-key failed to detect a response (response set 3% vs non-response set 3%), trials with an incorrect or disfluent naming response (response set 2% vs non-response set 2%), and trials with an RT below 350ms or above 2,000ms (response set 0% vs non-response set 0.1%). This led to a data loss of 5% in the Response set condition and 5% in the Non-response set condition. Mean naming latencies and the percentage of errors per condition are presented in Table 3. To test whether response set membership significantly influenced response times, a repeated measures ANOVA and Bayes factor calculation was performed on RTs in JASP (version 0.8.2; Wagenmakers et al., 2017). For interpretation of the Bayes factors the classification scheme provided in Wagenmakers et al. (2017) was used.

A significant main effect of the distractor condition was observed $F_1(1,19) = 14.83$, $p < .001$, $F_2(1,39) = 10.33$, $p = .003$. There was no significant effect of response set membership $F_1(1,19) = .04$, $p = .852$, $BF_{10} = 0.23$, $F_2(1,39) = 0.03$, $p = .869$, $BF_{10} = 0.17$, with the Bayes factor suggesting moderate evidence in favour of the null hypothesis. No significant interaction was observed between distractor condition and response set membership $F_1(1,19) = .22$, $p = .644$, $BF_{10} = 0.34$, $F_2(1,39) = 0.28$, $p = .598$, $BF_{10} = 0.23$, with the Bayes factor suggesting anecdotal evidence in favour of the null hypothesis. The typical interference effect was observed; RTs were longer for items with semantically related distractors ($M = 809.88$) compared to unrelated distractors ($M = 788.55$), $t_1(19) = 3.89$, $p < .001$, $d = 0.87$; $t_2(39) = 3.25$, $p = .002$, $d = 0.451$.

Planned t-test revealed a significant semantic interference for the Response set member condition ($t_1(19) = 2.93$, $p = .009$, $d = 0.66$; $t_2(39) = 2.91$, $p = .006$, $d = 0.46$),

Table 3. Mean RT in ms (95% confidence intervals in parentheses) and percentage of naming errors (including disfluencies) per condition.

| | Response set members (CI) | Error | Non-response set members (CI) | Error |
|-----------------------|---------------------------|-------|-------------------------------|-------|
| Related | 812 (769-855) | 2% | 808 (769-855) | 3% |
| Unrelated | 788 (750-829) | 2% | 790 (754-822) | 2% |
| Semantic interference | 24 | | 18 | |

and for the Non-response set member condition ($t_1(19) = 2.18, p = .042, d = 0.49$; $t_2(39) = 2.04, p = .048, d = 0.32$). A direct comparison between the magnitude of the semantic interference effects revealed no significant difference between the Response set and Non-response set membership conditions $t_1(19) = 0.47, p = 0.644, d = 0.11, BF_{10} = 0.26$ $t_2(39) = 3.25, p = 0.002, d = 0.08, BF_{10} = 0.19$, with the Bayes factor suggesting moderate evidence in favour of the null hypothesis.

3.2. fMRI data

Group-averaged parameters of the 20 participants were less than 1 mm motion and 1° rotation, consistent with previously reported sparse fMRI acquisitions (e.g. Gracco et al., 2005).

3.2.1. A priori defined ROI analyses

ROI analyses contrasting the Response membership and Non-response membership condition (both directions) yielded no significant activation clusters. Per response set membership condition, related and unrelated distractor conditions were contrasted. The Related > Unrelated contrast revealed significant activation clusters in the posterior STG and the MTG within the Response set member condition using the pMTG/STG ROI spheres at $-57, -57, -3$ and $-60, -30, 3$ (resp. de Zubicaray et al., 2013; de Zubicaray & McMahon, 2009) and the superior and posterior temporal gyrus ROIs from the Hammer-smith atlas (see Figure 1 panel A). No significant activation clusters were observed in the Non-response set membership condition. A plot of the activation pattern in the pMTG for the response set conditions revealed a similar pattern of activation for both related to semantic interference, which was larger for the Response set membership condition (see Figure 2).

As no main effect of response set membership was observed, we contrasted the related and unrelated distractor conditions pooled over the response set membership conditions. The Related > Unrelated contrast revealed a significant activation cluster in the posterior middle temporal gyrus and LIFG (pars orbitalis) using the pMTG ROI centred on $-57, -57, -3$ (de Zubicaray et al., 2013) and an LIFG ROI centred on $-51, 24, -9$ (de Zubicaray & Mahon, 2009. See Figure 1 panel B for a rendering of the significant activation clusters). No significant clusters were observed for the Unrelated > Related contrast. An overview of the significant activation clusters is presented in Table 4.

3.2.2. Exploratory whole brain analysis

Finally an exploratory whole brain analysis was carried out applying the same contrasts as above. No significant

activation clusters were observed in any of the contrasts beyond the ROI analysis.

4. Discussion

The current study set out to investigate whether LIFG involvement in lexico-semantic retrieval is a function of the co-activation levels of lexical candidates for potential selection. Specifically we tested whether the level of distractor-target co-activation in the PWI task influenced LIFG engagement by manipulating response set membership (e.g. Piai et al., 2012; Roelofs, 1992). As neurobiological accounts of lexical selection in spoken word production assume a prominent role for the LIFG during lexico-semantic retrieval, we predicted that greater co-activation strength among candidates in the response set compared to non-response set membership condition would differentially recruit LIFG as well as left MTG/STG.

In both response set conditions, the typical semantic interference effect was observed, with longer RTs for semantically related distractor words compared to unrelated distractor words. However, the magnitude of the semantic interference effect did not differ significantly between response set conditions. This finding runs counter to the co-activation assumptions made by lexical-selection-by-competition (Piai et al., 2012; Roelofs, 1992) and post-lexical selection accounts (Mahon et al., 2007) that predict stronger and weaker semantic interference, respectively, but it is consistent with an earlier null finding by Caramazza and Costa (2000; Experiment 3). To our knowledge, Caramazza and Costa's study is the only other study to directly compare response set membership within the one PWI experiment just as we did. Those authors argued that the co-activation assumption lacked empirical support (see also Caramazza & Costa, 2001). Our findings similarly challenge the co-activation assumption. Prior work attempting to influence co-activation in semantic interference via manipulations of semantic feature overlap have also proved equivocal at best (e.g. Mahon et al., 2007; see Gauvin et al., 2018 for a review). Thus, a possible reason why we failed to observe differential fMRI activity in either pMTG or LIFG for the response set manipulation is that the co-activation assumption is wrong, i.e. activation levels did not differ between the respective SI effects, so that engagement of these regions was equivalent across conditions.

Surprisingly, semantic interference was associated with a relative *increase* in activation in the posterior middle and superior temporal gyri in the related condition compared to the unrelated condition. This pattern of activation in pMTG/STG differs to previous

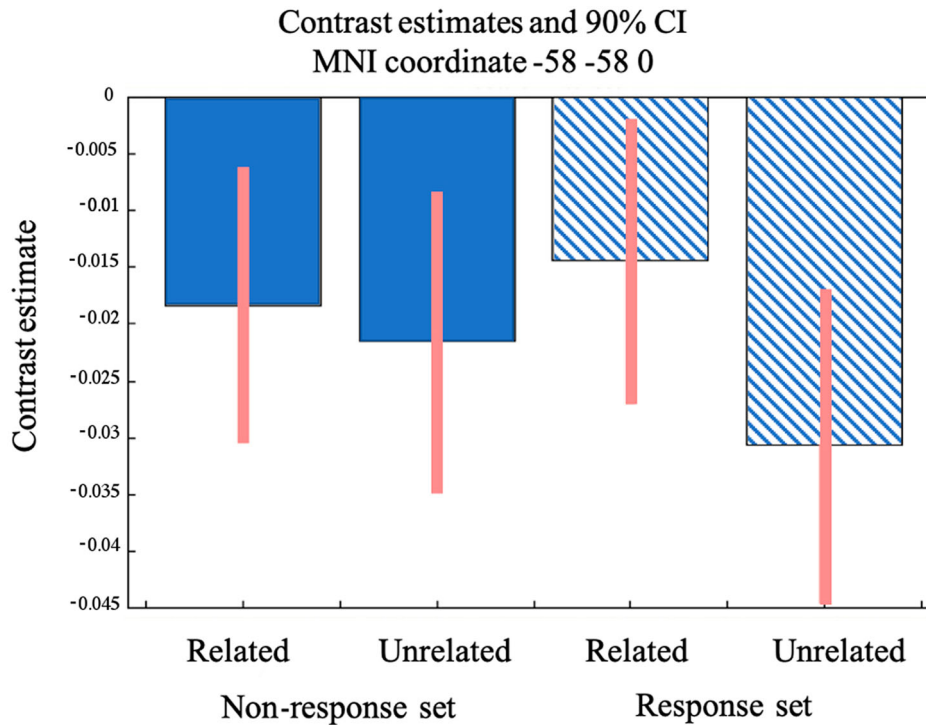


Figure 2. Plot of parameter estimates in the peak voxel for semantic interference (Related > Unrelated) in the pMTG across Response set and Non-response set conditions.

neuroimaging studies of semantic interference in PWI tasks employing similar designs, in which a signal *decrease* was observed in the same region (Abel et al., 2012; de Zubicaray et al., 2009, 2013; Piai et al., 2013, 2014). A likely explanation for this difference in directionality is that the current study incorporated both response set and non-response set members in the one design. Unlike response set distractor words that were also target picture names and so familiarised prior to the experiment and named throughout, the non-response set distractor items were presented only during the experiment and so were relatively novel. It is well known that BOLD signal responses to repeated items are reduced relative to novel items, the so-called *repetition suppression* effect (Grill-Spector et al., 2006). However, a potential caveat to this explanation is that

repetition suppression effects in fMRI studies have been demonstrated to be contingent on items being attended to (e.g. Henson & Mouchlianitis, 2007), whereas in the PWI procedure, participants are instructed to ignore the word while naming the picture (see de Zubicaray et al., 2013 for discussion).

We failed to observe significant LIFG activity associated with semantic interference in either response set condition, consistent with some findings from prior fMRI studies with the PWI paradigm (e.g. de Zubicaray et al., 2013; Piai et al., 2013). Significant LIFG involvement was observed when the data were pooled across the two conditions, consistent with other PWI studies (Abel et al., 2009; de Zubicaray et al., 2009). That the LIFG activity was only significant when data were pooled across conditions suggests its detection required more statistical power compared to the pMTG that showed significant activity for semantic interference with fewer items. It is therefore possible that previously reported studies lacked sufficient power to reliably detect LIFG signal changes. If this interpretation is correct, then this might be because LIFG involvement in this task has a relatively smaller effect size than pMTG, raising questions about the prominent roles afforded to it as either enhancing lexical activation or resolving *lexico-semantic* competition in neurobiological accounts (Heim et al., 2009; Oppenheim et al., 2010; Roelofs, 2018; Schnur et al., 2009; Thompson-Schill et al., 1997; Thompson-Schill

Table 4. Cerebral regions showing significant activation as a function of the response set membership and semantic relatedness of the distractor condition.

| Contrasts | Peak MNI (x y z) | Z Score | Cluster Size (Voxels) |
|--|------------------|---------|-----------------------|
| <i>Response set Related > Unrelated</i> | | | |
| left posterior STG ^a | -64 -32 14 | 4.82 | 78 |
| left pMTG ^a | -58 -58 0 | 3.82 | 80 |
| <i>Related > Unrelated All</i> | | | |
| left IFG (pars orbitalis) ^a | -46 22 -10 | 3.36 | 34 |
| left pMTG ^a | -60 -60 2 | 3.32 | 12 |

^a ROI corrected.

et al., 1998; Thompson-Schill et al., 1999). Certainly, it is not as prominent as the more reliably observed pMTG. Alternatively, the relatively reduced effect in LIFG might reflect field inhomogeneities in BOLD signal detection caused by the differences of magnetic susceptibility of air and tissue that may result in local image distortions and signal losses particularly in orbital frontal cortex. Notably, we observed significant BOLD activity in the pars orbitalis of the LIFG only after pooling our data. However, this explanation seems less likely as our fMRI acquisition protocol included field mapping and an optimal TE of 26 ms and spatial resolution to correct for these issues (e.g. Weiskopf et al., 2007).

The present study also suggests further delineation of the role of LIFG in top down control in neurobiological language production models. Considerable research has shown LIFG comprises distinct subregions, both structurally (e.g. pars orbitalis, pars opercularis and pars triangularis, corresponding to Brodmann areas 47, 44 and 45, respectively) and functionally. After pooling our data, we observed significant activity in the pars orbitalis consistent with previous PWI studies of semantic interference (e.g. de Zubicaray & McMahon, 2009). Meta-analyses of fMRI studies have also confirmed an important role for this LIFG subregion in control processes during lexico-semantic competition more broadly (e.g. Bourguignon & Gracco, 2019).

The current study should not be interpreted as implying the LIFG is *not* involved in top-down modulation of *linguistic* interference, as previous reports of LIFG involvement in the PWI task consistently noted activity when the unrelated/incongruent distractor condition was contrasted with a congruent (i.e. identity) distractor or lexical control condition (such as a row of Xs; e.g. Abel et al., 2012; de Zubicaray & McMahon, 2009; Gauvin et al., 2019). Some previous studies contrasting Related > Unrelated and neutral distractors also observed increased activation in the superior frontal gyrus, preSMA or ACC (Abel et al., 2012; de Zubicaray et al., 2013; Piai et al., 2013, 2014). This was typically interpreted to reflect conflict detection, selection and top-down control mechanisms. In the current study no significant activation clusters were observed in these areas for any of the contrasts.

5. Conclusions

The current study investigated the role of the LIFG in top-down control of lexico-semantic retrieval within a PWI experiment in which we attempted to manipulate lexical coactivation via the response set membership of distractor words. The behavioural and fMRI data demonstrated a significant semantic interference effect.

However semantic interference did not differ between response set conditions, thus failing to support the coactivation assumption. Semantic interference was associated with a significant BOLD signal increase in the left pSTG and MTG, with the combined data revealing additional significant activation in the LIFG. Our findings support a prominent role for the pMTG during lexico-semantic retrieval, but suggest LIFG involvement comprises a relatively smaller effect, thus questioning the prominent role afforded to it in some neurobiological models of language production.

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