

# Neural evidence for a separation of semantic and phonological control processes

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**Running title:** Neural separation of language control

## Abstract

There remain major doubts about the nature and domain specificity of inhibitory control processes, both within and between cognitive domains. This study examined inhibitory processes within the language domain, by contrasting semantic versus phonological inhibitory control. In an fMRI experiment, elderly participants performed phonological and semantic inhibitory control tasks involving resistance to highly or weakly interfering stimuli. In the semantic domain, inhibitory control effects, contrasting high vs. low interference control levels, were observed at univariate and multivariate levels in all fronto-parieto-temporal region-of-interests. In the phonological domain, inhibitory control effects were observed only at multivariate levels, and were restricted to the pars triangularis of the bilateral inferior frontal gyrus and to the left middle temporal gyrus. Critically, no reliable multivariate cross-domain prediction of neural patterns associated with inhibitory control was observed. This study supports a functional dissociation of the neural substrates associated with inhibitory control for phonological vs. semantic domains.

149 words

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## **1. Introduction**

Language processing is not only characterized by specific sets of linguistic representations, but also by various processes that control the way information is activated and deactivated within these representational bases. Inhibitory control is one of these processes. Lack of verbal inhibitory control occurs regularly in everyday life, and manifests itself for example by verbal paraphasias such as saying ‘pass’ for ‘glass’ or ‘vase’ for ‘glass’, these intrusion errors being phonologically and/or semantically related to the target word. However, the exact nature of verbal inhibitory processes, and particularly their level of specificity, remains an open question. The aim of the present study is to contrast semantic vs. phonological inhibitory control and to determine whether inhibitory control in these two verbal domains is supported by common or distinct neural mechanisms.

At the behavioral level, a number of neuropsychological studies have documented patients with language control impairment, but the specificity of this impairment is still strongly debated. On the one hand, several studies have investigated verbal control abilities in patients with semantic aphasia (Barde et al., 2006; Chertkow et al., 1997; Jefferies & Lambon Ralph, 2006). Semantic aphasia is characterized by a multi-modal semantic impairment associated with lesions in the left prefrontal or temporo-parietal cortices. Patients with semantic aphasia exhibit impaired performance in various verbal and non-verbal semantic tasks (such as naming, category fluency, word-picture matching or visual semantic association tasks), intrusion errors in spontaneous speech and poor comprehension in the context of fluent speech. Critically, performance appears to be largely influenced by inhibitory control requirements of the tasks (i.e. ease of identifying relevant association and rejecting distractors) (Corbett et al., 2009). For example, patients with semantic aphasia can find a specific semantic concept in a naming task but not when several semantic concepts are activated and need to be compared and when distractors need to be inhibited such as in a

semantic association judgment task. While this inhibitory control impairment is considered to characterize mainly semantic processing in these patients, control of other language dimensions such as phonological processing has been rarely directly investigated. We know that performance for phonological levels of processing is most often preserved as assessed via word repetition or naming tasks (Cuetos et al., 2000; Howard et al., 2015; Jefferies & Lambon Ralph, 2006; Soni et al., 2009), but the inhibitory control demands of these tasks are generally low. More broadly, few neuropsychological studies have directly contrasted semantic and phonological inhibitory control. One of the few studies is a study by Barde et al. (2010) which assessed the performance of 20 aphasic patients on a recent negative task, i.e. a working memory probe recognition task involving negative probes that are either semantically or phonologically related to one of the target words. This task measures phonological and semantic control in an indirect manner, by assuming that phonologically and semantically related probes create interference that needs to be resisted to. Barde et al. observed distinct patient profiles, with some patients being more sensitive to phonological than semantic distractors, and vice-versa for other patients, suggesting that phonological and semantic inhibitory control may involve distinct processes. Another task developed to assess phonological and semantic inhibitory control, particularly in spoken word production, is the blocked cyclic naming task (Abdel Rahman & Melinger, 2009; Damian et al., 2001). Participants have to repeatedly name a small set of pictures either in a semantically homogeneous block (e.g. *apple, pear, orange, banana*) or a semantically heterogeneous block (e.g. *apple, table, dog, car*); repeated naming of the pictures from the homogeneous block is supposed to build up proactive interference that needs to be inhibited, as compared to repeated naming in the heterogeneous block. This effect, the blocking effect, materializes in slower naming responses for pictures from homogenous versus heterogeneous blocks. Studies using this paradigm generally observed different responses profiles for semantically (words from

the same semantic category) vs. phonologically (words sharing a number of phonemes) homogeneous blocks, with increased latencies for semantic blocks but diminished latencies for phonological blocks (Abdel Rahman & Melinger, 2009; Belke et al., 2017; Damian & Bowers, 2003; Damian et al., 2001; Roelofs, 1999; Wang et al., 2018 but see Damian & Dumay, 2009 for an interference effect in phonological condition). Other paradigms, based on the inhibition of an automatically activated representation as via priming paradigms, are particularly prone to assess more purely language inhibitory control. In priming paradigms, participants have to read or make a lexical decisions for verbal item, leading to faster responses to a target word when a semantically or phonologically related prime stimulus has been presented shortly before (see for a review, Hutchison, 2003). The prime stimulus is considered to automatically activate or pre-activate all representations that are phonologically or semantically similar. If the task context makes that these automatically activated representations interfere with the target information (because of being different from the active representations), then inhibitory control processes need to intervene. One of these is the Picture-word Interference (PWI) task where a to-be-named picture is presented along with a phonological or semantic distractor word. The automatically activated phonological and semantic representations associated with the distractor word needs to be inhibited when naming the target word (note however that there may be facilitory effects at the sublexical phonological level) (De Zubicaray & McMahon, 2009; see Nozari & Pinet, 2020 for a review of the PWI effect; Schriefers et al., 1990). These studies suggest again distinct processes involved in semantic and phonological inhibitory control.

At the neuroimaging level, the literature reveals the same uncertainties. On the one hand, there is general agreement about the involvement of the left inferior prefrontal cortex in inhibitory cognitive control in the form of resistance to interference (e.g., D'Esposito et al., 1999; Fedorenko & Blank, 2020; Feredoes et al., 2006; Jonides et al., 1998; Swick et al.,

2008; Thompson-Schill et al., 2002). But it is unclear to what extent the function of the inferior prefrontal cortex needs to be further subdivided as a function of the material on which inhibitory cognitive control is applied, also because very few neuroimaging studies have contrasted phonological vs. semantic inhibitory control, or verbal vs. non-verbal inhibitory control requirements. Studies focusing on semantic inhibitory control generally highlighted the involvement of the left inferior frontal gyrus (IFG) but also of temporo-parietal cortices including the middle temporal gyrus (MTG) during tasks such as picture naming, semantic association (with close semantic distractors) judgment, picture-word-interference or semantic blocking (Abel et al., 2009; De Zubicaray et al., 2013; Schnur et al., 2009; Whitney et al., 2011). Also, patients with aphasia demonstrating a specific deficit for this type of tasks demonstrated lesions in these areas (Gardner et al., 2012; Hoffman et al., 2011; Jefferies & Lambon Ralph, 2006; Thompson-Schill et al., 2002). Neuroimaging studies focusing on phonological inhibitory control as assessed with a phonological association task (picture-word with close phonological distractors) also highlighted the involvement of the IFG, in both anterior (BA45) and posterior (BA44) parts, as well as of temporal cortices (including posterior superior and middle temporal gyri) (Marian et al., 2014; Peramunage et al., 2011; Righi et al., 2010; Xie & Myers, 2018).

Very few studies have compared phonological and semantic inhibitory control processes, with furthermore inconsistent results. Early neuroimaging studies, without directly confronting phonological and semantic inhibitory control processes, reported a functional distinction within the left IFG, with ventral anterior parts of the IFG being involved more specifically in semantic tasks, and the dorsal posterior part supporting language inhibitory control more generally, including phonological levels of inhibitory control (Devlin et al., 2003; Gough et al., 2005; Poldrack et al., 1999; Snyder et al., 2007; Wagner et al., 2001). More recently, Klaus and Hartwigsen (2019) demonstrated a double dissociation between semantic

(category) and phonological (rhyme generation) fluency tasks, with a disruption of semantic fluency performance when repetitive transcranial magnetic stimulation was applied over the anterior IFG, and with facilitation of the phonological fluency performance when repetitive transcranial magnetic stimulation was applied over the posterior IFG. However, these results are somewhat difficult to interpret in terms of inhibitory control only given the multi-determined nature of verbal fluency tasks (access to semantic vs. phonological information, monitoring of already produced words requiring updating and working memory demands, ...). Another study also observed dissociations, but between frontal and temporo-parietal regions rather than between anterior and posterior inferior frontal cortices, by observing in left brain-damaged patients that inferior frontal lesions were associated with inhibition deficits for semantic neighbours in a word-production task while posterior superior temporal and inferior parietal lobe lesions were associated with inhibition deficits for phonological neighbours (Mirman & Graziano, 2013). However, a meta-analysis study observed a similar involvement of a left anterior IFG cluster (BA45) for phonological and semantic processes, based on a large set of studies involving a large set of tasks such as rhyme generation, synonym generation and translation, verbal fluency, semantic retrieval, word repetition, synonym production, lexical decision, inner speech generation, and semantic categorisation tasks (Liakakis et al., 2011). Again, these results are difficult to interpret in terms of inhibitory control given the heterogeneous and multi-determined nature of the different tasks included in this meta-analysis, some tasks having stronger inhibitory demands (e.g., verbal fluency) than others (e.g., word repetition).

A few studies contrasted phonological and semantic inhibitory control in language tasks in a more targeted manner. Minicucci et al. (2013) manipulating the phonological or semantic nature of distractor prime words in a lexical decision task and observed a similar modulation of the IFG, the MTG and the superior temporal gyrus (STG) for the inhibition of both prime

types in healthy participants. Also, a study using an fMRI adaptation paradigm with tasks involving difficulty-matched phonological and semantic inhibitory control tasks showed similar adaptation effects for the anterior and posterior IFG (BA45/47 and BA44) during phonological and semantic inhibitory control, supporting common neural substrates for semantic and phonological control (Gold et al., 2005). However, in these studies, phonological inhibitory demands were manipulated via stimuli having a lexico-semantic content (i.e., words instead of nonwords), raising the possibility that the phonological inhibitory conditions also had a lexico-semantic inhibitory component. Other studies using this more targeted approach on inhibitory control did observe differences between phonological and semantic inhibitory control. Abel et al. (2009) contrasted brain activity for auditory distractor words that shared phonological or semantic features with the target word in a picture naming task. While observing common IFG involvement in both inhibitory control conditions, associated networks differed: a fronto-temporal neural network, including the MTG, characterized the semantic inhibitory control condition while a fronto-parietal neural network, including the angular gyrus (AG), characterized the phonological inhibitory control condition. But once more, this study used words as phonological distractors leading to an ambiguous interpretation of results. A further study observed a functional subdivision of IFG involvement for inhibitory control in phonological (with words and nonwords) versus semantic judgment tasks (Snyder et al., 2007): now the anterior part of the IFG (BA 45) was associated with phonological inhibitory control while the posterior part (BA44) was associated with semantic inhibitory control. These results contrast with the earlier neuroimaging studies that associated anterior IFG with semantic inhibitory control and posterior IFG with phonological control. Furthermore, Snyder et al. observed that phonological inhibitory control for words only involved the IFG while phonological inhibitory control for nonwords involved the precuneus and supramarginal areas. This study



therefore questions more generally the involvement of the IFG in pure phonological inhibitory control. Finally, a study using the blocked cyclic naming task, assessing build-up of semantic or phonological interference and associated inhibitory control demands during repeated object naming observed that left IFG activation was specific to semantic interference while the left temporal cortex (left STG and MTG) was involved in both phonological and semantic blocking conditions (Schnur et al., 2009). But again, the latter results are difficult to interpret due to the use of lexical stimuli (words) in both phonological and semantic inhibitory conditions.

In sum, while a number of studies appear to show a distinction between phonological and semantic inhibitory control processes at the behavioural and neural level, other studies do not support such a distinction. Furthermore, the role of the IFG, or distinct subparts of the IFG, in phonological inhibitory control is highly uncertain. These inconsistencies may either reflect the task-specificity of phonological vs. semantic inhibitory control processes and their complexity, or an insufficient control of stimulus and task parameters when assessing phonological vs. semantic inhibitory control. In the studies discussed here, either structurally different tasks were used, not allowing for a direct comparison between phonological and semantic inhibitory control demands, or the tasks did not target in a sufficiently pure manner phonological vs. semantic aspects of inhibitory control by using lexical stimuli (words) for testing both aspects of control.

The aim of this study was to maximize the contrast between phonological and semantic material on which inhibitory control processes had to act, and therefore we used nonwords for the phonological task and words for the semantic task. Both tasks were constructed to be structurally as similar as possible but to clearly differ at the linguistic level at which inhibitory control processes need to intervene. Using word stimuli would have rendered the phonological and semantic control tasks more similar at the content level, but there was a risk

that similar lexical inhibitory processes could then be engaged in both conditions, leading to a less optimal situation for contrasting phonological vs. semantic inhibitory control. We used a semantic judgment task that had been frequently used in previous studies for examining semantic inhibitory control deficits (Schnur et al., 2009) and further adapted it to phonological material by using nonwords and phonological judgments. In the semantic variant of this paradigm, participants were presented with two target words and two test words and they needed to select the test word that provides the best semantic match with both of the target words. Furthermore, in the high inhibitory control condition, the wrong test word was preactivated via a prime word presented shortly before the appearance of the target words, and hence the preactivated test word needed to be inhibited to allow for correct response selection. We adapted this task to a phonological judgment condition, in which participants had to decide which of two test nonwords provided the best phonological match with the two target nonwords, a wrong test nonword having been preactivated via a prime nonword presented briefly before the presentation of the target nonwords (see Figure 1). The two tasks also had a low inhibitory control condition, in which the prime word/nonword preactivated the correct target word/nonword. By contrasting the high versus low inhibitory control conditions for the two task versions, we aimed at isolating and comparing the neural substrates associated with semantic and phonological inhibitory control. A further specificity of this study was the use of both univariate and multivariate fMRI approaches in order to assess the neural commonality and specificity of semantic and phonological inhibitory control with a high level of sensitivity. In the multivariate approach, we examined whether the multivariate neural patterns supporting semantic inhibitory control predict those involved in phonological inhibitory control and vice versa. A positive prediction would provide a strong argument for at least a certain degree of neural overlap of semantic and phonological inhibitory control. We used auditory nonwords and visual words as primes in order to maximize the contrast of

phonological vs. semantic pre-activation. This design choice was based on behavioural piloting of the task which had shown that visual nonwords did not lead to a strong phonological preactivation effect. Besides, the use of an auditory presentation of the prime maximize the chance to use a phonological process rather than a simple visual letter form process to find similarity between nonwords, strategy probably easier than the phonological one when we processing words with no meaning. Moreover, this is consistent with previous studies, the vast majority of studies assessing semantic control also used written words while studies assessing phonological inhibitory control generally use auditory prime (Damian & Martin, 1999; Jescheniak & Schriefers, 2001; Mahon et al., 2007). Furthermore, these differences in presentation modalities of the tasks should not affect the results given that we contrasted within-task levels of inhibitory control and then used these contrasts for further analyses. This design choice allowed for an even stronger test of the domain-general hypothesis of verbal inhibitory control: if inhibitory processes are domain general, then associated multivariate patterns should be similar, whether information has been presented auditorily or visually. A region-of-interest (ROI) strategy was used, by focusing on the different parts of the IFG, the AG and the MTG areas highlighted in previous studies on semantic and/or phonological inhibitory control. Finally, the inclusion of elderly participants also allowed to assess the question of the commonality/specificity of semantic vs. phonological inhibitory control processes with maximal sensitivity given the increased interindividual differences in inhibitory control processes that appear during aging and the resulting higher likelihood of observing dissociations between both inhibitory control processes if they rely on distinct neural and cognitive substrates (Janse & Adank, 2012; Lustig et al., 2008; Salthouse, 2009; Tun et al., 2002). Note that this report is part of a larger, open-ended preregistered research project on semantic and phonological inhibitory control in

healthy and brain-damaged populations (<https://osf.io/jcx9t/>). All data are available in the OSF project.

## **2. Methods**

### **2.1. Participants**

Thirty-four right-handed French-speaking elderly adults (19 women) with no history of neurological disorder, sensory impairment, or learning, were recruited, in accordance with the sample size ( $N=30$ ) and statistical power thresholds (power = .80; effect size = .75;  $\alpha=.001$ ) determined during preregistration via fMRIPower (fmripower.org) for the specific inhibitory control contrasts task as specified below. Participants received 10 euros per hour for their participation. Data from three participants (2 women) were excluded because of excessive movement in the scanner (i.e. see criteria below). The data from 31 participants (18 women) were retained for further analysis (mean age =  $60.12 \pm 6.08$  years old, age range = 50-72). All participants were screened for signs of cognitive decline using the Mattis Dementia Rating Scale (Mattis, 1988). All participants scored above the cut-off (cut-off score = 123; Turner et al., 2013) (mean =  $142.87 \pm 2.22$ ; range = 133 to 144). Participants were also screened for language impairment with a naming task (EXaDé from Bachy-Langedock, 1989). All participants obtained a score close to the maximum (mean =  $35.58 \pm 0.76$ ; range = 33 to 36). For all participants, exclusion criteria were a history of psychiatric disease, premorbid/developmental language disorders or any medical contraindication for accessing an MRI environment. All participants gave their written informed consent before participating to the study. The ethics committee of the Faculty of Medicine and the University Hospital (Comité d'éthique hospitalo-universitaire, ULiège) had approved the study.

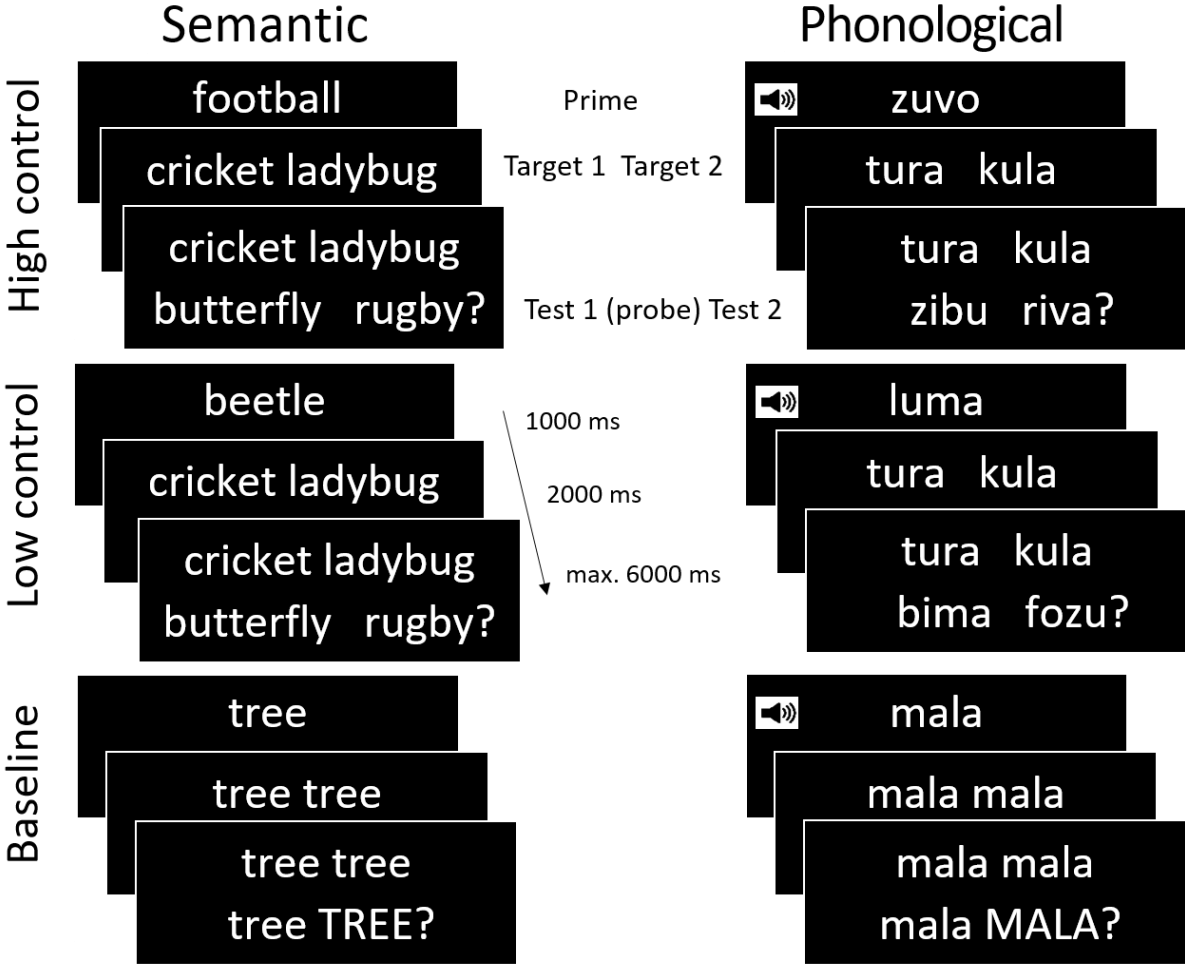
### **2.2. fMRI task description**

Semantic and a phonological language inhibitory control tasks were administered in separate blocks during a unique fMRI session (see Figure 1). The two tasks followed the same structure, with the presentation of a visual prime word during 1000 ms for the semantic

inhibitory control task and the presentation of an auditory prime nonword for the phonological inhibitory control task. Note that contrary to the indication of visual presentation for the prime nonword in the preregistration report, the prime nonword was presented auditorily in order to maximize preactivation of phonological information. Next, the two target (non)words were presented during 2000 ms followed by the additional appearance of two test (non)words at the bottom of the screen. The participant had to decide within 6000 ms which test (non)word provided the best match with both target (non)words. The participants responded by pressing the button under their index finger for selecting the test (non)word on the left of the screen and the button under their middle finger for selecting the (non)word on the right of the screen. The initial prime (non)word either interfered (high inhibitory control) or facilitated (low inhibitory control) with the selection of the correct test (non)word. More precisely, to manipulate semantic inhibitory control demands, one of the two target words was polysemic (e.g. cricket in Figure 1), with only one of the two meanings being shared between the two words (e.g. *insect*). In the high inhibitory control condition, the prime (e.g., *football* to activate the semantic category of *sport*) activated the non shared meaning of the polysemic word and one of the test words further corresponded to this non-target meaning (e.g. *rugby*); thus high inhibitory control was needed to inhibit both the initially activated semantic concept and the distractor test word (Test 2 in Figure 1). On the other hand, in the low inhibitory control condition, the prime (e.g., *beetle* to activate the semantic category of *insect*) already activated the shared semantic concept, and was furthermore aligned with the correct test word (*butterfly* in the example); thus selection of the correct target word was facilitated and did not require any inhibition. A full list of the material is given in Table 1 of the Appendix. A baseline condition controlling for perceptual and motor aspects was also included, the same word appearing for each stimulus type only the font differing between the target and test

words; the participant had to select the test word presented in the same font as both target words.

Figure 1. Illustration of the semantic and phonological inhibitory control tasks, for high inhibitory control, low inhibitory control and baseline conditions. (single column fitting image)



The phonological inhibitory control task had exactly the same structure and rationale but involved phonological judgments for nonwords, the participants being asked to select the test nonword that shared a vowel and its position with both target nonwords (see Figure 1). The two bisyllabic target nonwords (e.g., tura – kula) shared their vowels but only one of the vowels was informative for response selection. In the high inhibitory control condition, only the non-informative vowel was preactivated via a prime nonword that shared the non-informative vowel (e.g., zuvo) of the target nonwords and its position as well as both vowels

of the incorrect test nonword (e.g., **fozu**). This test nonword had to be inhibited for selecting the correct test nonword that shared a vowel and its position with both target nonwords (e.g., **bima**), the informative vowel /a/ which furthermore had not been pre-activated by the prime word. For the low inhibitory control condition, the prime nonword shared both vowels with the two target nonwords and one vowel and its position with the correct test nonword, facilitating its selection. The prime nonwords, presented auditorily, had been recorded by a female voice at a normal speech rate of one nonword per 800ms approximately. A full list of the material is given in Table 1 of the Appendix. All letters/sounds used had unambiguous and systematic grapheme-phoneme correspondences. Again, a baseline condition controlling for perceptual and motor aspects was included and also involved font matching judgments. For each task there were 26 trials per inhibitory control condition and 18 baseline trials (corresponding to 35% of the entire task). During preregistration, a slightly higher number of trials had been planned but when piloting the task, we considered it more appropriate to reduce the number of trials by a small proportion (10 to 13%) in order to keep time in the scanner and task duration acceptable for elderly participants. The duration of the intertrial interval was variable (random Gaussian distribution centered on a mean duration of  $7000 \pm 1000$  ms) and further varied as a function of the participants' response times since the probe array disappeared immediately after a response was recorded. If the participant did not respond within 6000 ms, 'no response' was recorded and the next trial began. Both response accuracy and response times were collected. Each task was presented in two different blocks in the same session, and the order of the blocks was randomly assigned to participants. A T1 structural brain scan was acquired between the two tasks (see below). A practice session outside the magnetic resonance environment, prior to the start of the experiment, familiarized the participants with the specific task requirements and included the administration of 4 practice trials for each task which could be repeated; this procedure ensured that each

participant demonstrated sufficient understanding of the task before being placed in the scanner. Specific lists were used for the practice trials in order to avoid item repetition and learning effects that could interact with the inhibitory control demands of the experimental trials. The task was presented on a workstation running Matlab 12 and the Cogent toolbox (UCL, <http://www.vislab.ucl.ac.uk/cogent.php>).

### **2.3. MRI acquisition**

Functional MRI time series were acquired on a whole-body 3T scanner (Magnetom Prisma, Siemens Medical Solutions, Erlangen, Germany) operated with a 20-channel receiver head coil. Multislice T2\*-weighted functional images were acquired with the multi-band gradient-echo echo-planar imaging sequence (CMRR, University of Minnesota) using axial slice orientation and covering the whole brain (32 slices, multiband factor = 2, FoV = 192x192 mm<sup>2</sup>, voxel size 3x3x3 mm<sup>3</sup>, 25% interslice gap, matrix size 64x64x32, TR = 978 ms, TE = 30 ms, FA = 90°). The five initial volumes were discarded to avoid T1 saturation effects. A gradient-recalled sequence was applied to acquire two complex images with different echo times (TE = 10.00 and 12.46 ms respectively) and generate field maps for distortion correction of the echo-planar images (EPI) (TR = 634 ms, FoV = 192x192 mm<sup>2</sup>, 64x64 matrix, 40 transverse slices (3 mm thickness, 25% inter-slice gap), flip angle = 90°, bandwidth = 260 Hz/pixel). For anatomical reference, a high-resolution T1-weighted image was acquired for each subject (T1-weighted 3D magnetization-prepared rapid gradient echo (MPRAGE) sequence, TR = 1900 ms, TE = 2.19 ms, inversion time (TI) = 900 ms, FoV = 256x240 mm<sup>2</sup>, matrix size = 256x240x224, voxel size = 1x1x1 mm<sup>3</sup>). Between 1020 and 1131 functional volumes were acquired (M = 1069.71, SD = 32.48) during the semantic inhibitory control task. For the phonological inhibitory control task, between 903 and 1081 functional volumes (M = 969.61, SD = 48.39) were acquired. The visual stimuli were



displayed on a screen positioned at the rear of the scanner, which the participant could comfortably see through a mirror mounted on the standard head coil.

## **2.4. fMRI analyses**

### **2.4.1. Image preprocessing**

The functional images were preprocessed and analysed at the univariate level using SPM12 software (Wellcome Department of Imaging Neuroscience, [www.fil.ion.ucl.ac.uk/spm](http://www.fil.ion.ucl.ac.uk/spm)) implemented in MATLAB (Mathworks, Inc., Sherborn, MA). EPI time series were corrected for motion and distortion using the Realign and Unwarp with default settings functions together with the FieldMap toolbox (implemented in SPM12) (Andersson et al., 2001; Hutton et al., 2002). A mean realigned functional image was then calculated by averaging all the realigned and unwrapped functional scans and the structural T1 image was coregistered to this mean functional image (using a rigid body transformation optimised to maximise the normalised mutual information between the two images). The mapping from subject to MNI space was estimated from the structural image with the “unified segmentation” approach (Ashburner & Friston, 2005). The warping parameters were then separately applied to the functional and structural images to produce normalised images of resolution  $2 \times 2 \times 2$  mm<sup>3</sup> and  $1 \times 1 \times 1$  mm<sup>3</sup>, respectively. Finally, the warped functional images were spatially smoothed with a Gaussian kernel of 4 mm FWHM to improve signal-to-noise ratio while preserving the underlying spatial distribution (Schrouff et al., 2012); this smoothing also diminishes the impact residual head motion can have on MVPA performance, even after head motion correction (Gardumi et al., 2016). We screened extreme head motion by excluding the *entire* data set of a participant if whole session movement was larger than 3 mm / 3° and/or if there was a peak movement exceeding 3 mm / 3° relative to initial head position. This resulted in the removal of the data of three participants (see above).

### **2.4.2. Univariate analyses**

Univariate analyses isolated BOLD signal variations associated with the inhibitory control effect in each task. For each participant BOLD responses were estimated at each voxel, using a general linear model with epoch regressors and event-related regressors. For both tasks, the regressor ranged from the onset of the probe display to the participant's response, where the inhibitory control, high or low is required. On this basis, for each task, two linear contrast were performed, one for the high inhibitory control condition (minus the baseline condition) and another for the low inhibitory control condition (minus the baseline condition). For each model, the design matrix also included the realignment parameters to account for any residual movement-related effect. A high-pass filter was implemented using a cut-off period of 128 sec in order to remove the low-frequency drifts from the time series. Serial autocorrelations were estimated with a restricted maximum likelihood algorithm with an autoregressive model of order 1 (+ white noise). However, even if the TR we used was still close to 1 second, the autoregressive model used in SPM might not be optimal for fMRI data collected with a TR of less than 1 second (Sahib et al., 2016). Therefore, we also checked our data by using the FAST option (recommended for fast TRs; Olszowy et al., 2019) for autocorrelation estimation and modelling in SPM. This did not lead to any change in group-level results, as expected since inadequate AR modelling impacts mainly fixed effect analyses but not group level analyses.

For both tasks, we extracted beta values for each level of inhibitory control (High-Baseline and Low-Baseline) for the different regions of interest defined later in the section 2.4.5. Then, we conducted a repeated measures ANOVA 2 (phonological vs. semantic domain) X 2 (high vs. low inhibitory control) on betas for each ROI.

We also assessed functional connectivity for the two inhibitory control tasks as a function of level of control via psychophysiological interaction analysis. We took the left anterior (pars opercularis) and posterior (pars triangularis) IFG ROIs as seed regions (see below) given that

these regions had been most commonly involved in verbal inhibitory control in the previous studies reviewed in the Introduction section. These regions were also found to be sensitive to phonological and semantic control effects in the multivariate results reported below.

Functional connectivity analysis (psychophysiological interaction) as implemented in SPM uses a seed-voxel approach and we therefore defined specific coordinates for these ROIs that allowed to extract associated volumes of interest. These specific coordinates were defined based on the peak coordinates obtained in the high control conditions, by averaging across the phonological and semantic contrasts. The resulting coordinates for the left IFG seed regions were the following: IFG triangularis [+50, 32, 20], IFG opercularis [+38, 22, 0]. For each subject, a linear model was constructed for each task and included three regressors (plus the realignment parameters as covariates of no interest). A first regressor represented level of inhibitory control, by contrasting the high and the low conditions. The second regressor represented the activity in the seed area. The third regressor represented the interaction of interest between the first (psychological) and second (physiological) regressors. Significant results for psychophysiological interaction regressor indicated similar changes in the regression coefficients between the seed area and reported brain areas, as a function of level of inhibitory control. After smoothing (6-mm FWHM Gaussian kernel), the contrast images for this regressor were then entered in a second-level (random effects) analysis. A one-sample t test was performed to assess group-level changes in functional connectivity as a function of level of inhibitory control (voxelwise threshold,  $P < 0.05$  corrected for whole brain volume, or small volume corrections at  $P < 0.05$  for a priori locations of interest).

### **2.4.3. Multivariate analyses**

In order to use the most sensitive analyses for detecting inhibitory control condition effects but also for assessing the similarity of neural substrates supporting semantic vs. phonological inhibitory control, multivariate analyses were conducted using PRoNT<sub>o</sub>, a pattern recognition

toolbox for neuroimaging ([www.mlnl.cs.ucl.ac.uk/pronto](http://www.mlnl.cs.ucl.ac.uk/pronto); Schrouff et al., 2013). We determined the voxel patterns discriminating between both inhibitory control conditions, for each task at an individual subject level. We trained classifiers to distinguish voxel activity patterns associated with high inhibitory control versus low inhibitory control in the preprocessed and 4-mm smoothed functional images for each task events separately, using a binary support vector machine (Burges, 1998). For within-task classifications of level of inhibitory control, a leave-one-block-out (LOBO) cross-validation procedure was used. For cross-tasks predictions of level of inhibitory control, a leave-one-run-out (LORO) cross-validation procedure was used, resulting in training the inhibitory control classifier on one task (e.g., phonological task) and testing the classifier on the other task (e.g., semantic task). Classifier performance was tested by comparing the group-level distribution of classification accuracies to a chance-level distribution using one sample t tests.

#### **2.4.4. ROI analyses**

The present study focused on the main ROIs discussed in the first section, including the IFG, the MTG and the AG. These ROIs were defined and delimited using IBASPM 71 and IBASPM 116 atlases (<http://www.thomaskoenig.ch/Lester/ibaspm.htm>) via the wfupickatlas toolbox. They were exported as .nifti files and then used as an inclusive mask for voxels on which the univariate and multivariate analyses were conducted. For all ROIs we considered both hemispheres. A first ROI was the IFG given its highly frequent involvement in phonological and semantic inhibitory control (Abel et al., 2009; Fiebach et al., 2007; Gagnepain et al., 2008; Gold et al., 2005; Ralph et al., 2016; Rissman et al., 2003; Sabri et al., 2008; Seghier et al., 2010; Snijders et al., 2009; Snyder et al., 2007; Visser et al., 2012; Whitney et al., 2011). In line with the literature, we considered separately the pars opercularis (BA44), the pars triangularis (BA45) and the pars orbitalis (BA47). Another ROI frequently associated with semantic control was the (posterior) MTG (Jedidi et al., 2021; Jefferies et al.,

2006, 2020). Finally, a last ROI was the AG, as it has also been reported to be sensitive to inhibitory control effects (Abel et al., 2009; Klepousniotou et al., 2014; Snyder et al., 2007). Note that the two latter regions were not initially mentioned in the preregistration report but were subsequently deemed essential for a comprehensive assessment of this study's research question given their frequent involvement in language inhibitory control as reported in the literature. Moreover, based on a comprehensive literature review, we choose to use a slightly more fine-grained division of the IFG in three segments rather than two segments (anterior-posterior) initially mentioned in the preregistration report.

### **2.5. Behavioral analyses**

To assess the behavioural effects of the inhibitory control conditions, we conducted a 2 (phonological vs. semantic domain) X 2 (high vs. low inhibitory control) repeated measures ANOVA on response accuracy as well as on response times. Significant effects were further followed up by Paired t-tests.

### **2.6. Complementary Bayesian statistical approach**

Although not initially planned during preregistration, we also report results for Bayesian statistical analyses for both behavioral and fMRI data, in order to appreciate evidence both *in favor* and *against* effects of interest while frequentist statistics only allow to interpret evidence in favor of these effects (Wagenmakers, 2007). The  $BF_{10}$  value represents the result of the likelihood ratio of the alternative model ( $H1$ ) relative to the null model ( $H0$ ); the likelihood ratio of  $H0$  relative to  $H1$  corresponds to the reverse,  $BF_{01} = 1/BF_{10}$ . The following classification of evidence strength was used (Jeffreys, 1961; Lee & Wagenmakers, 2014): A BF of 1 provides no evidence,  $3 > BF > 1$  provides anecdotal evidence,  $10 > BF > 3$  provides moderate evidence,  $30 > BF > 10$  provides strong evidence,  $100 > BF > 30$  provides very strong evidence, and  $BF > 100$  provides extreme/decisive evidence. Bayesian analyses were

conducted with Version 0.10.2.0 of the JASP software package, using default settings for the Cauchy prior distribution (JASP Team, 2017, jasp-stats.org).

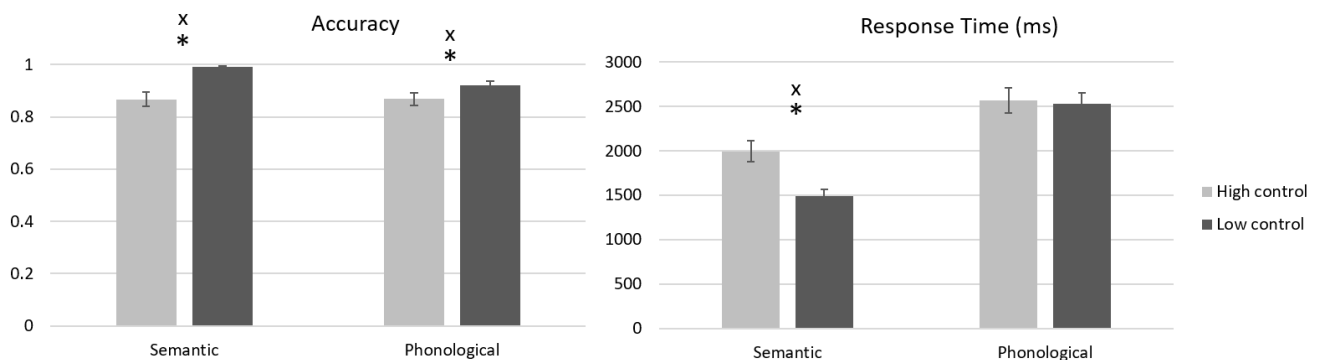
### 3. Results

#### 3.1. Behavioral analyses

Descriptive data are presented in Figure 2. A first 2 (phonological vs. semantic domain) X 2 (high vs. low inhibitory control) repeated measures ANOVA was conducted on response accuracy. The results showed no main effect of domain,  $F(1, 30)=2.13$ ,  $p=.16$ ,  $\eta^2_p=.07$ ;  $BF_{10}=0.69$ , but a main effect of inhibitory control,  $F(1, 30)=26.98$ ,  $p<.001$ ,  $\eta^2_p=.47$ ;  $BF_{10}=1702.58$ , indicating that the high inhibitory control condition led to the expected accuracy decrease relative to the low inhibitory control condition. Moreover, we observed a significant interaction between the domain and inhibitory control effects,  $F(1, 30)=5.61$ ,  $p=.024$ ,  $\eta^2_p=.16$ ;  $BF_{10}=1845.74$ , the inhibitory control effects being less important for the phonological domain (see Figure 2). Paired t-tests between the two levels of inhibitory control for each domain, after Bonferroni corrections for multiple comparisons ( $\alpha=.025$ ), confirmed a significant inhibitory control effect for the semantic domain ( $t=4.17$ ,  $p<.001$ ,  $d=0.75$ ;  $BF_{10}=116.96$ ) and for the phonological domain ( $t=4.22$ ,  $p<.001$ ,  $d=0.76$ ;  $BF_{10}=132$ ). When conducting the same ANOVA on response times, we observed a main effect of domain,  $F(1, 30)=47.78$ ,  $p<.001$ ,  $\eta^2_p=.61$ ;  $BF_{10}=1.04E+12$ , with slower response times for the phonological domain, a main effect of level of inhibitory control,  $F(1, 30)=23.74$ ,  $p<.001$ ,  $\eta^2_p=.44$ ;  $BF_{10}=2.19$ , as well as a significant interaction between domain and inhibitory control effects,  $F(1, 30)=32.01$ ,  $p<.001$ ,  $\eta^2_p=.52$ ;  $BF_{10}=2.48E+14$ . Paired t-tests showed a significant effect of inhibitory control in the semantic,  $t=5.76$ ,  $p<.001$ ,  $d=1.03$ ;  $BF_{10}=6831.10$ , but not in the phonological domain,  $t=0.83$ ,  $p=.41$ ,  $d=0.15$ ;  $BF_{10}=0.26$ . This absence of effect was confirmed by a BF in favor of the null model- $H_0$  ( $BF_{01}=3.79$ ). In sum, we observed a main

effect of inhibitory control for both accuracy and response times in the semantic domain and only for accuracy in the phonological domain.

Figure 2. Behavioral data of both control tasks assessed in fMRI. The stars indicate significant inhibitory control effects ( $p_{\text{Bonferroni}} < .025$ ) while the cross signs indicate Bayesian evidence in favour of a difference with a  $\text{BF}_{10} > 3$ . (Single column fitting image)



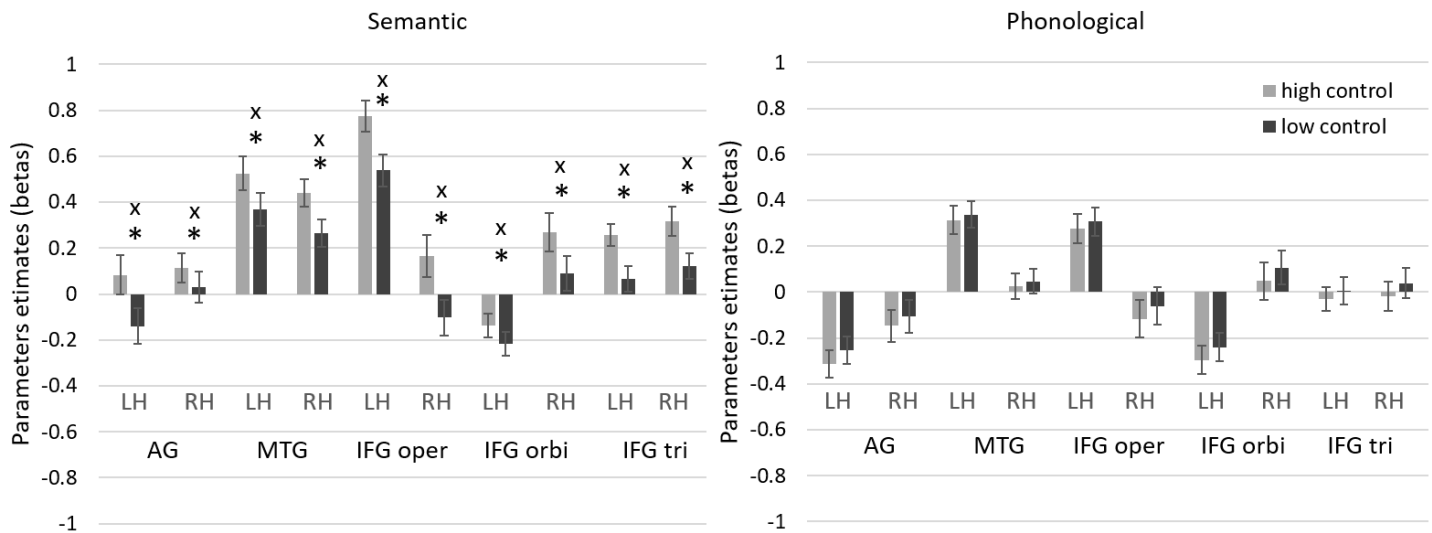
We further checked that the constant appearance of the question mark on the right side of the screen had not biased participant's responses towards the rightward test word. A Bayesian paired t-test on response accuracy and response times as a function of correct test word location showed no impact of correct-test-word location on response accuracy (left side: mean=0.95±0.06; right side: mean=0.95±0.06;  $\text{BF}_{10}=0.19$ ) or response times (left side: mean=1457.32±388.21; right side: mean=1501.09±412.49;  $\text{BF}_{10}=0.48$ ) for the semantic task and a small leftward instead of a rightward advantage for the phonological control task and only for response accuracy (left side: mean=0.92±0.09; right side: mean=0.90±0.09;  $\text{BF}_{10}=46.8$ ) and not for response times (left side: mean=2065.29±557.61; right side: mean=2153.96±564.22;  $\text{BF}_{10}=1.12$ ).

### 3.2. Neuroimaging - Univariate Analyses

To analyse univariate control and domain effects, we extracted for each ROI beta values as a function of level of control (High-baseline vs. Low-baseline) and domain (semantic vs. phonological) (see 2.4.2 section for details) (see Figure 3). A repeated measures 2 (domain) X

2 (level of control) ANOVA was conducted on the beta values for each ROI. Results are detailed in Table 2 of the Appendix. We observed a main effect of domain for all ROIs, except for the IFG - pars opercularis, the right MTG and the right AG, semantic judgment leading to overall higher beta values than phonological judgment. With regard to the main inhibitory control effect, all ROIs exhibited a main effect of control except for the bilateral MTG. All ROIs were also characterized by a significant interaction.

Figure 3. Betas extracted from the different ROIs for each control level in both domains. The stars indicate classification significantly higher than chance-level ( $p_{\text{Bonferroni}} < .005$ ). The cross signs indicate Bayesian evidence in favour of a difference with a  $\text{BF}_{10} > 3$ . (2-column fitting image)



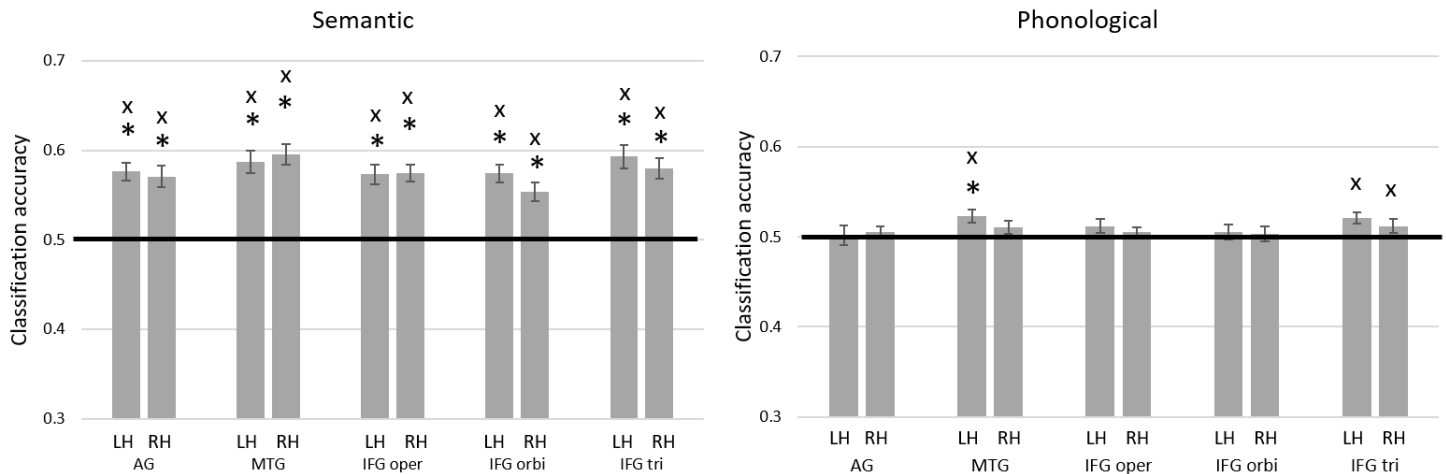
Paired t-tests demonstrated an effect of control in all ROIs during semantic judgment but not in any ROIs during phonological judgment, after Bonferroni corrections for multiple comparisons ( $\alpha = .005$ ). Bayesian paired t-tests confirmed evidence in favour of inhibitory control effects in all ROIs for the semantic task but not for the phonological task (see Table 2 in the Appendix and Figure 3). Also, evidence in favour of the *absence* of an inhibitory control effect was observed for the phonological task in the left IFG – pars opercularis and orbitalis (respectively,  $\text{BF}_{01} = 3.03$  and  $\text{BF}_{01} = 3.70$ ).

### 3.3. Neuroimaging - Multivariate Analyses



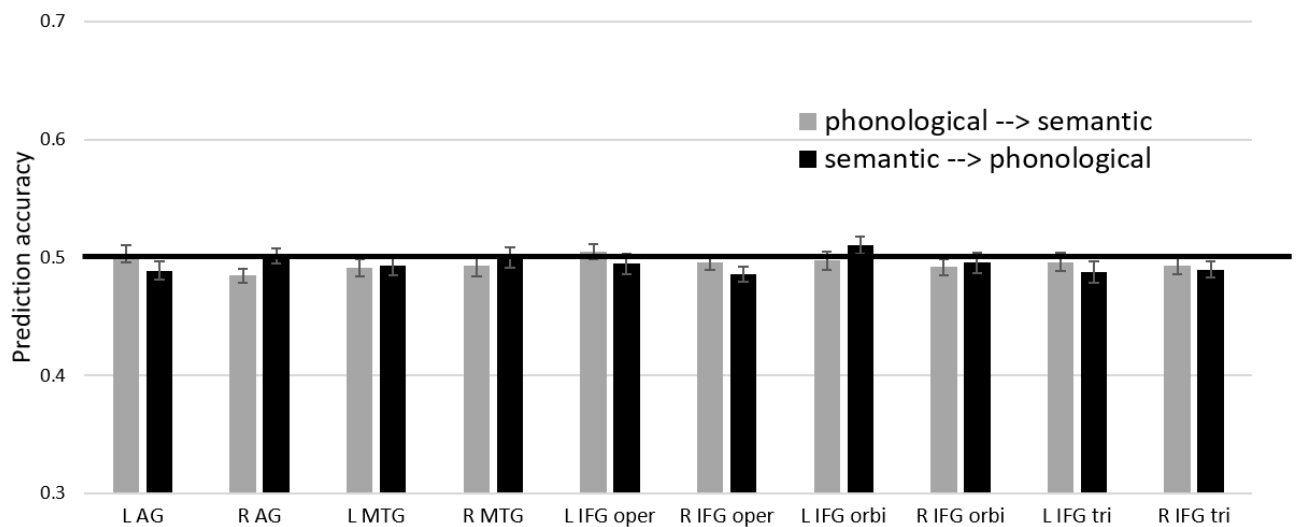
Next, we examined multivariate control effects in order to assess neural responses to inhibitory control in the most sensitive manner for each ROI and critically, to determine whether the same multivariate neural responses characterize control effects in the semantic and phonological domain using within-domain classification and between-domain prediction approaches of effects-of interest (see section 2.4.3 for details). First, regarding within-domain classifications of control effects for the semantic domain, significant above-chance level classification of level of control was observed in all ROIs including the three parts of the IFG, pars opercularis, orbitalis and triangularis as well as in the bilateral MTG and AG. These significant classifications were confirmed by Bayesian one sample t-tests (see Table 3 in the Appendix and Figure 4). For the phonological task, we observed significant above-chance level classifications of control effects only in the left MTG ( $p < .005$ ). Bayesian one sample t-tests demonstrated evidence in favour of above-chance level classifications for the left MTG and the bilateral IFG triangularis (see Table see Table 3 in the Appendix and Figure 4). Evidence in favour of the *absence* of above-chance level classifications was observed for the left AG, the right IFG opercularis and the bilateral IFG orbitalis with (see Table 3 in the Appendix and Figure 4).

Figure 4. Classification rates for level of inhibitory control, as function of ROIs and domains. The black line bar marks chance-level classification rates. The stars indicate classification significantly higher than chance-level with Bonferroni corrections for multiple comparisons ( $p_{\text{Bonferroni}} < .005$ ). The cross signs indicate evidence in favour of above-chance-level classifications at  $BF_{10} > 3$ . (1.5 column fitting image)



These results indicate robust classification of level of inhibitory control for all ROIs in the semantic task, but only for the left MTG and the bilateral IFG – pars triangularis, in the phonological task. In a final, critical analysis, we examined whether the multivariate neural patterns allowing to distinguish level of inhibitory control in the semantic task are the same as those involved in the phonological task. Although this prediction, if existing, was only expected for the left MTG and the bilateral IFG – pars triangularis showing multivariate control effects in both tasks, the cross-task predictions were run for all ROIs for sake of completeness. This analysis (see Figure 5 and Table 4 in the Appendix) did not lead to any significant cross-domain prediction of inhibitory control effects. Moreover, Bayesian statistics showed evidence in favour of the *absence* of reliable cross-domain prediction of inhibitory control effects in all ROIs.

Figure 5. Predictions rates for level of inhibitory control, as function of ROIs and domains. The black line bar marks the chance-level. (1.5 column fitting image)



### 3.4. Psychophysiological interactions

Finally, to further understand the dynamics of inhibitory control processes, we explored functional connectivity for the left IFG - pars triangularis and the left IFG – pars opercularis as seed areas, via psychophysiological interaction. In the semantic domain, the left IFG opercularis was functionally connected to the bilateral IFG triangularis, IFG orbitalis and the AG as well as with the right MTG. The left IFG triangularis was associated with the left IFG opercularis and the right IFG orbitalis, the AG as well as the bilateral MTG. In the phonological domain, a more restricted functional network was observed, with the left IFG triangularis being associated with the right MTG and the right AG only. The left IFG opercularis seed was not functionally connected to any other region.

## 4. Discussion

This study examined the commonality of the univariate and multivariate neural substrates associated with verbal inhibitory control, by comparing semantic and phonological domains in elderly healthy participants. By using structurally identical tasks for measuring semantic and phonological inhibitory control, we observed behavioral inhibitory control effects for

response accuracy in both tasks. At the univariate neural level, only a semantic inhibitory control effect was reliably observed in all frontal and temporal ROIs. At the multivariate neural level, high and low inhibitory control conditions could be decoded in all frontal and temporal ROIs for the semantic task; for the phonological task, inhibitory control conditions could be decoded in a slightly more restricted set of ROIs including the bilateral IFG pars triangularis, and the left MTG. Crucially, no evidence for between-domain prediction of neural patterns associated with inhibitory control was observed in any ROI. Functional connectivity analyses further demonstrated that semantic control was associated with an extensive fronto-parieto-temporal network, including the three segments of the IFG; phonological control was associated with a more restricted fronto-parieto-temporal network including the left IFG triangularis, the right AG and the right MTG.

On the one hand, the present data are in line with a number of studies on semantic control, by supporting the role of the bilateral IFG, the MTG and the AG (Badre & Wagner, 2005; Binder et al., 2009; Davey et al., 2016; Jefferies & Lambon Ralph, 2006; Jefferies et al., 2020; Noonan et al., 2010; Rodd et al., 2005; Seghier et al., 2010; Thompson-Schill et al., 1999; see Ralph et al., 2016 for a recent review). These results have been observed with different paradigms, all requiring inhibitory control of semantic abilities, such as picture-naming task, semantic associative judgement tasks or build-up of semantic interference during speech production (Abel et al., 2009; Schnur et al., 2009; Whitney et al., 2011). In contrast to previous studies, we observed that all three subregions of the IFG were sensitive to semantic inhibitory control, while numerous previous studies suggested a more specific involvement in semantic inhibitory control for the anterior segment of the IFG (Devlin et al., 2003; Gardner et al., 2012; Gough et al., 2005; Poldrack et al., 1999; Snyder et al., 2007; Thompson et al., 2015; Wagner et al., 2001). The posterior part of the IFG, corresponding to the pars opercularis, had been suggested to reflect higher cognitive control demands rather than being

specific to semantic control (Duncan, 2010; Fedorenko et al., 2012; Vigneau et al., 2006). However, our data are not in line with this assumption as the pars opercularis did not reliably distinguish between high and low control levels in the phonological inhibitory control task. Moreover, we demonstrated that the IFG pars opercularis, the IFG pars triangularis, the AG and the MTG formed a functional network during semantic inhibitory control. While the AG region has been considered to play a more specific role in semantic search and comparison processes (Abel et al., 2009; Mechelli et al., 2007; Seghier et al., 2010; Snyder et al., 2007), the IFG and the MTG areas may reflect representation-driven semantic inhibitory control processes. Jedidi et al. (2021) indeed recently observed IFG and pMTG involvement in implicit semantic control processes using a passive listening, adaptation fMRI paradigm, and in which there were no task-related explicit control requirements.

For the phonological domain, we observed a rather restricted involvement of frontal and temporal ROIs in inhibitory control as compared to previous studies (Marian et al., 2014; Peramunage et al., 2011; Righi et al., 2010; Schnur et al., 2009; Xie & Myers, 2018).

Furthermore, reliable neural inhibitory control effects were only observed in multivariate analyses. As already noted, these analyses showed inhibitory-control-sensitive neural patterns in the anterior part of the IFG (pars triangularis) but not in the more posterior part of the IFG (pars opercularis). While one previous study also observed anterior rather than posterior IFG involvement in phonological inhibitory control processes (Snyder et al., 2007), other studies, have also found involvement of the posterior part of the IFG (Devlin et al., 2003; Gough et al., 2005; Klaus & Hartwigsen, 2019; Mirman & Graziano, 2013; Poldrack et al., 1999; Snyder et al., 2007; Wagner et al., 2001). This restricted involvement of the anterior part of the IFG in phonological inhibitory control processes may be due to the use of word stimuli in these other studies, the posterior IFG having been associated lexical rather than sublexical levels of processing (Noonan et al., 2013; Teige et al., 2019). In most previous studies,

phonological inhibitory demands were manipulated via stimuli having a lexico-semantic content raising the possibility that the larger neural effects observed in these studies may have been the consequence of a combined recruitment of phonological and semantic control processes. Only one study assessed phonological control with nonwords and contrasted it with phonological control for words (Snyder et al., 2007). They also observed a more restricted set of areas involved in phonological control for nonwords as compared to words, with only the word stimuli eliciting left IFG recruitment. It should however be noted that the nonword condition was supposed to involve lesser inhibitory control demands than the word condition which involved the judgment of vowels whose sublexical phonological characteristics could be in conflict with the lexical phonological word form while this could not be the case for the nonword stimuli. In other words, the left IFG involvement in the study by Snyder et al. for phonological inhibitory control was also influenced by lexico-semantic processes. This interpretation is also supported by a study by Minicucci et al. (2013), showing left IFG involvement for phonological control only when the target stimuli were associated with a large number of lexical competitors. In sum, our results indicate that when phonological inhibitory control demands are clearly distinguished from lexical-semantic inhibitory control demands, then IFG involvement in phonological inhibitory control processes is strongly reduced and limited to multivariate neural effects in the anterior part (pars triangularis). One question we need to address here is whether our phonological inhibitory control task, although targeting more purely sublexical phonological inhibitory control demands than did previous studies, may have been characterized by overall lesser inhibitory control demands relative to the semantic inhibitory control task. This is not likely to be the case given that reaction times were overall slower in the phonological task indicating that this task was actually more challenging than the semantic task. It could then be argued that the low control condition of the phonological task may have had an already high inhibitory control demand,

reducing the likelihood of observing differential inhibitory control effects when comparing the high and low control conditions. However, if this would have been the case, then already the low control phonological condition should have been associated with high beta values in the univariate analyses. As shown in Figure 2, this was not the case, both phonological control conditions being characterized by relatively small beta values as compared to the semantic control conditions for the different ROIs.

The most critical finding of this study is the fact that despite the common involvement of the bilateral IFG pars triangularis and the left MTG in both semantic and phonological inhibitory control in this study, the multivariate neural signals supported by these regions during phonological and semantic inhibitory control appeared to be distinct. Indeed, no cross-domain prediction of inhibitory control was observed in these areas (or in any other area). Therefore, it is a possibility that the inhibitory process required for phonological domain was lower than for the semantic domain and thus reflect a difference in the amount of inhibitory control.

However, the potentially lesser involvement of inhibitory control processes should be due to the nature of phonological control rather than to the task or the stimuli per se. Indeed, as already highlighted, our results are actually in line with previous results that showed a more restricted behavioural effect as well as brain network for phonological vs. semantic inhibitory control abilities while also using nonword stimuli but structurally very different tasks (Snyder et al., 2007; Minicucci et al., 2013). Also, despite the fact that the network involved in phonological inhibitory control was more restricted than the one involved in semantic inhibitory control, there were still significant phonological control effects in the left MTG and the left IFG triangularis, bilaterally as in the semantic inhibitory control condition. But the multivariate patterns were not the same as no significant between-task prediction of level of control was observed. This qualitative difference suggests that the patterns involved do not encode the same differences or the same intensity of differences. This study was indeed the

first to use a multivariate approach for comparing the neural substrates associated with semantic and phonological inhibitory processes. Our findings extend those of previous studies by showing that the commonality of univariate brain responses in fronto-temporal cortices identified in a number of studies for phonological and semantic inhibitory control cannot be taken as evidence for domain-general inhibitory control processes (Abel et al., 2009; Gold et al., 2005; Liakakis et al., 2011; Minicucci et al., 2013; Schnur et al., 2009). Overall, our data support the smaller set of studies that suggested a neural dissociation between semantic and phonological inhibition, and refine the conclusions of these studies by showing that dissociations can even be observed within ROIs recruited both by phonological and semantic inhibitory control. Our results indicate that IFG pars triangularis and left MTG are specialized for inhibitory control of both phonological and semantic information, but likely via distinct processing or representational properties. A possible interpretation of this functional dissociation within the same neural substrates could be that the MTG serves a representational function of target and co-activated stimulus features, which can be of phonological or lexico-semantic nature, depending on the task. The IFG pars triangularis would then serve a selection process, selecting the phonological or lexico-semantic target representation and inhibiting non-target, co-activated representations and features. In that case, the neural signals would differ for phonological and semantic inhibitory control tasks within the same neural regions as qualitatively different types of representation will be co-activated and inhibited in the two situations. Furthermore, it is likely that lexico-semantic stimuli, due to their associated familiarity and multi-dimensional knowledge (at auditory, visual, motor, emotional levels), will elicit larger sets of co-activated information and more widespread patterns of activation than purely phonological stimuli such as nonwords which only integrate sublexical orthographic and phonological representations (Ralph et al., 2016). This latter assumption is



also in line with the much broader fronto-temporal network identified in the present study for the semantic than the phonological inhibitory control tasks.

This two-stage and two-state interpretation of our findings would not be inconsistent with the controlled semantic cognition (CSC) framework (Jefferies et al., 2020; Ralph et al., 2016; Thompson et al., 2018) which also distinguishes representational from selection/inhibitory aspects of linguistic control, although only for the semantic domain. Ralph et al. (2016) indeed argue that the left MTG area may represent integrated semantic information stemming from different sources (first stage) while the IFG pars triangularis (see for a review, Noonan et al., 2013) would be more particularly involved in selection of target information (second stage). A recent computational model using a reverse-engineering approach (Jackson et al., 2021) also includes these two stages, with a multimodal representation hub linking information from sparsely connected modality-specific regions, and a control process operating on peripheral rather than deep semantic network layers. The latter needs to preserve the flexibility required for thinking and acting as the situation demands. Importantly, while these two models have been developed specifically for semantic control, our data suggest that these fronto-temporal control networks are involved in both phonological and semantic control situations, but functionally dissociate in terms of internal representations and selection/inhibitory control processes involved when operating on phonological vs. semantic linguistic information.

Note that there was a general task difference in the paradigm used in this study by presenting nonwords in one case and words in the other case, with furthermore the prime nonwords being presented auditorily and the prime words being presented in written format. At the same time, it is important to mention that the main contrasts on which our results are based did not involve direct contrasts between the two tasks, but second-level comparisons of within-task inhibitory control effects; the within-task level-of-inhibitory-control effects should neutralize

the general phonological vs semantic processing differences as these contrasts involve the same linguistic levels of processing and only level-of-inhibitory control that is required differs between the two conditions to-be-compared. Critically, we intended to examine a strong hypothesis of the commonality of phonological and semantic control processes, by determining the univariate and multivariate similarities of the control processes despite these differences in stimulus material and modality. More generally, it proves to be very difficult to compare inhibitory control processes between domains in a perfectly pure and direct manner. One option, the one we took, is to maximally contrast the domains so that any commonality being identified can only be attributed to hypothetically shared inhibitory control processes. But one could argue that the experimental paradigm could in that case inflate the likelihood of detecting between-task differences due to these maximal between-domain and between-task differences (although note that we took care to avoid direct between domain comparisons for this reason). Indeed, a previous study has for example demonstrated that the nature of the linguistic stimuli used could moderate the existing link between language and non-linguistic executive control processes (Declerck et al., 2017). Another option is to use tasks and materials as similar as possible, such as words for both phonological and semantic judgment, but in that case commonalities may reflect the shared levels of representation and the necessarily shared associated inhibitory control processes intervening in the two task conditions rather than real cross-domain inhibitory control processes.

To conclude, the present study showed the recruitment of a broad fronto-temporal network for semantic inhibitory control. A subpart of this network also supported phonological inhibitory control while presenting distinct multivariate neural patterns in phonological vs. semantic inhibitory control situations. This study may reconcile the inconsistent findings of the current literature, by showing the involvement of partially common neural regions in phonological

and semantic inhibitory control but by highlighting also the functional dissociations within these regions as a function of phonological vs. semantic inhibitory control demands.

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## **CRedit author statement**

**Lucie Attout:** Conceptualization, Methodology, Formal analysis, Visualization, Investigation, Writing- Original draft preparation, Funding acquisition. **Steve Majerus:** Conceptualization, Methodology, Writing- Original draft preparation, Funding acquisition. **Coline Grégoire:** Investigation. **Pauline Querella:** Investigation.

[dataset] Attout, Lucie and Majerus Steve (2022), “Rehabilitation of language control in aphasia”, OSF: <https://osf.io/jcx9t/>

## References

- Abdel Rahman, R., & Melinger, A. (2009). Semantic context effects in language production: A swinging lexical network proposal and a review. *Language and Cognitive Processes*, 24(5), 713–734. <https://doi.org/10.1080/01690960802597250>
- Abel, S., Dressel, K., Bitzer, R., Kümmerer, D., Mader, I., Weiller, C., & Huber, W. (2009). The separation of processing stages in a lexical interference fMRI-paradigm. *NeuroImage*, 44(3), 1113–1124. <https://doi.org/10.1016/j.neuroimage.2008.10.018>
- Andersson, J. L., Hutton, C., Ashburner, J., Turner, R., & Friston, K. (2001). Modeling geometric deformations in EPI time series. *NeuroImage*, 13(5), 903–919. <https://doi.org/10.1006/nimg.2001.0746>
- Ashburner, J., & Friston, K. J. (2005). Unified segmentation. *NeuroImage*, 26(3), 839–851. <https://doi.org/10.1016/j.neuroimage.2005.02.018>
- Bachy-Langedock. (1989). *Batterie d'examen des troubles de la dénomination (ExaDé)*. Editions du Centre de Psychologie.
- Badre, D., & Wagner, A. D. (2005). Frontal Lobe Mechanisms that Resolve Proactive Interference. *Cerebral Cortex*, 15(12), 2003–2012. <https://doi.org/10.1093/cercor/bhi075>
- Barde, L. H. F., Schwartz, M. F., & Boronat, C. B. (2006). Semantic weight and verb retrieval in aphasia. *Brain and Language*, 97(3), 266–278. <https://doi.org/10.1016/j.bandl.2005.11.002>
- Barde, L. H. F., Schwartz, M. F., Chrysikou, E. G., & Thompson-Schill, S. L. (2010). Reduced short-term memory span in aphasia and susceptibility to interference: Contribution of material-specific maintenance deficits. *Neuropsychologia*, 48(4), 909–920. <https://doi.org/10.1016/j.neuropsychologia.2009.11.010>
- Belke, E., Shao, Z., & Meyer, A. S. (2017). Strategic origins of early semantic facilitation in the blocked-cyclic naming paradigm. *Journal of Experimental Psychology: Learning Memory and Cognition*, 43(10), 1659–1668. <https://doi.org/10.1037/xlm0000399>
- 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. <https://doi.org/10.1093/cercor/bhp055>
- Burges, C. J. C. (1998). A tutorial on support vector machines for pattern recognition. *Data Mining and Knowledge Discovery*, 2(2), 121–167. <https://doi.org/10.1023/A:1009715923555>
- Chertkow, H., Bub, D., Deaudon, C., & Whitehead, V. (1997). On the status of object concepts in aphasia. *Brain and Language*, 58(2), 203–232. <https://doi.org/10.1006/brln.1997.1771>
- Corbett, F., Jefferies, E., & Lambon Ralph, M. A. (2009). Exploring multimodal semantic control impairments in semantic aphasia: Evidence from naturalistic object use. *Neuropsychologia*, 47(13), 2721–2731. <https://doi.org/10.1016/j.neuropsychologia.2009.05.020>
- Cuetos, F., Aguado, G., & Caramazza, A. (2000). Dissociation of semantic and phonological

- errors in naming. *Brain and Language*, 75(3), 451–460.  
<https://doi.org/10.1006/brln.2000.2383>
- D’Esposito, M., Postle, B. R., Jonides, J., & Smith, E. E. (1999). The neural substrate and temporal dynamics of interference effects in working memory as revealed by event-related functional MRI. *Proceedings of the National Academy of Sciences of the United States of America*, 96(13), 7514–7519. <https://doi.org/10.1073/pnas.96.13.7514>
- Damian, M. F., & Bowers, J. S. (2003). Locus of semantic interference in picture-word interference tasks. *Psychonomic Bulletin and Review*, 10(1), 111–117.  
<https://doi.org/10.3758/BF03196474>
- Damian, M. F., & Dumay, N. (2009). Exploring phonological encoding through repeated segments. *Language and Cognitive Processes*, 24(5), 685–712.  
<https://doi.org/10.1080/01690960802351260>
- Damian, M. F., & Martin, R. C. (1999). Semantic and Phonological Codes Interact in Single Word Production. *Journal of Experimental Psychology: Learning Memory and Cognition*, 25(2), 345–361. <https://doi.org/10.1037/0278-7393.25.2.345>
- Damian, M. F., Vigliocco, G., & Levelt, W. J. M. (2001). Effects of semantic context in the naming of pictures and words. *Cognition*, 81(3), 77–86. [https://doi.org/10.1016/S0010-0277\(01\)00135-4](https://doi.org/10.1016/S0010-0277(01)00135-4)
- Davey, J., Thompson, H. E., Hallam, G., Karapanagiotidis, T., Murphy, C., De Caso, I., Krieger-Redwood, K., Bernhardt, B. C., Smallwood, J., & Jefferies, E. (2016). Exploring the role of the posterior middle temporal gyrus in semantic cognition: Integration of anterior temporal lobe with executive processes. *NeuroImage*, 137, 165–177.  
<https://doi.org/10.1016/j.neuroimage.2016.05.051>
- 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. <https://doi.org/10.1037/a0028717>
- De Zubicaray, G. I., & McMahon, K. L. (2009). Auditory context effects in picture naming investigated with event-related fMRI. *Cognitive, Affective and Behavioral Neuroscience*, 9(3), 260–269. <https://doi.org/10.3758/CABN.9.3.260>
- Declerck, M., Grainger, J., Koch, I., & Philipp, A. M. (2017). Is language control just a form of executive control? Evidence for overlapping processes in language switching and task switching. *Journal of Memory and Language*, 95, 138–145.  
<https://doi.org/10.1016/j.jml.2017.03.005>
- Devlin, J. T., Matthews, P. M., & Rushworth, M. F. S. (2003). Semantic processing in the left inferior prefrontal cortex: A combined functional magnetic resonance imaging and transcranial magnetic stimulation study. *Journal of Cognitive Neuroscience*, 15(1), 71–84. <https://doi.org/10.1162/089892903321107837>
- Duncan, J. (2010). The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. *Trends in Cognitive Sciences*, 14(4), 172–179.  
<https://doi.org/10.1016/j.tics.2010.01.004>
- Fedorenko, E., & Blank, I. A. (2020). Broca’s Area Is Not a Natural Kind. *Trends in Cognitive Sciences*, 24(4), 270–284. <https://doi.org/10.1016/j.tics.2020.01.001>
- Fedorenko, E., Nieto-Castañón, A., & Kanwisher, N. (2012). Syntactic processing in the

- human brain: What we know, what we don't know, and a suggestion for how to proceed. *Brain and Language*, 120(2), 187–207. <https://doi.org/10.1016/j.bandl.2011.01.001>
- Ferredoes, E., Tononi, G., & Postle, B. R. (2006). Direct evidence for a prefrontal contribution to the control of proactive interference in verbal working memory. *Proceedings of the National Academy of Sciences of the United States of America*, 103(51), 19530–19534. <https://doi.org/10.1073/pnas.0604509103>
- Fiebach, C. J., Friederici, A. D., Smith, E. E., & Swinney, D. (2007). Lateral inferotemporal cortex maintains conceptual-semantic representations in verbal working memory. *Journal of Cognitive Neuroscience*, 19(12), 2035–2049. <https://doi.org/10.1162/jocn.2007.19.12.2035>
- Gagnepain, P., Chételat, G., Landeau, B., Dayan, J., Eustache, F., & Lebreton, K. (2008). Spoken word memory traces within the human auditory cortex revealed by repetition priming and functional magnetic resonance imaging. *Journal of Neuroscience*, 28(20), 5281–5289. <https://doi.org/10.1523/JNEUROSCI.0565-08.2008>
- Gardner, H. E., Lambon Ralph, M. A., Dodds, N., Jones, T., Ehsan, S., & Jefferies, E. (2012). The differential contributions of pFC and temporo-parietal cortex to multimodal semantic control: Exploring refractory effects in semantic aphasia. *Journal of Cognitive Neuroscience*, 24(4), 778–793. [https://doi.org/10.1162/jocn\\_a\\_00184](https://doi.org/10.1162/jocn_a_00184)
- Gardumi, A., Ivanov, D., Hausfeld, L., Valente, G., Formisano, E., & Uludağ, K. (2016). The effect of spatial resolution on decoding accuracy in fMRI multivariate pattern analysis. *NeuroImage*, 132, 32–42. <https://doi.org/10.1016/j.neuroimage.2016.02.033>
- Gold, B. T., Balota, D. A., Kirchoff, B. A., & Buckner, R. L. (2005). Common and Dissociable Activation Patterns Associated with Controlled Semantic and Phonological Processing: Evidence from fMRI Adaptation. *Cerebral Cortex*, 15(9), 1438–1450. <https://doi.org/10.1093/cercor/bhi024>
- Gough, P. M., Nobre, A. C., & Devlin, J. T. (2005). Dissociating linguistic processes in the left inferior frontal cortex with transcranial magnetic stimulation. *Journal of Neuroscience*, 25(35), 8010–8016. <https://doi.org/10.1523/JNEUROSCI.2307-05.2005>
- Hoffman, P., Jefferies, E., & Lambon Ralph, M. A. (2011). Explaining semantic short-term memory deficits: Evidence for the critical role of semantic control. *Neuropsychologia*, 49(3), 368–381. <https://doi.org/10.1016/j.neuropsychologia.2010.12.034>
- Howard, D., Best, W., & Nickels, L. (2015). Optimising the design of intervention studies: critiques and ways forward. *Aphasiology*, 29(5), 526–562. <https://doi.org/10.1080/02687038.2014.985884>
- Hutchison, K. A. (2003). Is semantic priming due to association strength or feature overlap? A microanalytic review. In *Psychonomic Bulletin and Review* (Vol. 10, Issue 4, pp. 785–813). Springer New York LLC. <https://doi.org/10.3758/BF03196544>
- Hutton, C., Bork, A., Josephs, O., Deichmann, R., Ashburner, J., & Turner, R. (2002). Image distortion correction in fMRI: A quantitative evaluation. *NeuroImage*, 16(1), 217–240. <https://doi.org/10.1006/nimg.2001.1054>
- Jackson, R. L., Rogers, T. T., & Lambon Ralph, M. A. (2021). Reverse-engineering the cortical architecture for controlled semantic cognition. *Nature Human Behaviour*, 5(6), 774–786. <https://doi.org/10.1038/s41562-020-01034-z>

- Janse, E., & Adank, P. (2012). Predicting foreign-accent adaptation in older adults. *Quarterly Journal of Experimental Psychology*, 65(8), 1563–1585. <https://doi.org/10.1080/17470218.2012.658822>
- Jedidi, Z., Manard, M., Balteau, E., Degueldre, C., Luxen, A., Phillips, C., Collette, F., Maquet, P., & Majerus, S. (2021). Incidental Verbal Semantic Processing Recruits the Fronto-temporal Semantic Control Network. *Cerebral Cortex*, 31(12), 5449–5459. <https://doi.org/10.1093/cercor/bhab169>
- Jefferies, E., Crisp, J., & Ralph, M. a. L. (2006). The impact of phonological or semantic impairment on delayed auditory repetition: Evidence from stroke aphasia and semantic dementia. *Aphasiology*, 20(9), 963–992. <https://doi.org/10.1080/02687030600739398>
- Jefferies, E., & Lambon Ralph, M. A. (2006). Semantic impairment in stroke aphasia versus semantic dementia: A case-series comparison. *Brain*, 129(8), 2132–2147. <https://doi.org/10.1093/brain/awl153>
- Jefferies, E., Thompson, H., Cornelissen, P., & Smallwood, J. (2020). The neurocognitive basis of knowledge about object identity and events: dissociations reflect opposing effects of semantic coherence and control. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375(1791), 20190300. <https://doi.org/10.1098/rstb.2019.0300>
- Jeffreys, H. (1961). *Theory of probability*. Oxford, UK: Clarendon.
- Jescheniak, J. D., & Schriefers, H. (2001). Priming Effects from Phonologically Related Distractors in Picture—Word Interference. *The Quarterly Journal of Experimental Psychology Section A*, 54(2), 371–382. <https://doi.org/10.1080/713755981>
- Jonides, J., Schumacher, E. H., Smith, E. E., Koeppe, R. A., Awh, E., Reuter-Lorenz, P. A., Marshuetz, C., & Willis, C. R. (1998). The role of parietal cortex in verbal working memory. *Journal of Neuroscience*, 18(13), 5026–5034. <https://doi.org/10.1523/jneurosci.18-13-05026.1998>
- Klaus, J., & Hartwigsen, G. (2019). Dissociating semantic and phonological contributions of the left inferior frontal gyrus to language production. *Human Brain Mapping*, 40(11), 3279–3287. <https://doi.org/10.1002/hbm.24597>
- Klepousniotou, E., Gracco, V. L., & Pike, G. B. (2014). Pathways to lexical ambiguity: fMRI evidence for bilateral fronto-parietal involvement in language processing. *Brain and Language*, 131, 56–64. <https://doi.org/10.1016/j.bandl.2013.06.002>
- Lee, M. D., & Wagenmakers, E.-J. (2014). *Bayesian cognitive modeling: A practical course*. Cambridge university press.
- Liakakis, G., Nickel, J., & Seitz, R. J. (2011). Diversity of the inferior frontal gyrus—A meta-analysis of neuroimaging studies. *Behavioural Brain Research*, 225(1), 341–347. <https://doi.org/10.1016/j.bbr.2011.06.022>
- Lustig, C., Hasher, L., & Zacks, R. T. (2008). Inhibitory deficit theory: Recent developments in a “new view.” In *Inhibition in cognition*. (pp. 145–162). American Psychological Association. <https://doi.org/10.1037/11587-008>
- 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), 503–535.  
<https://doi.org/10.1037/0278-7393.33.3.503>

- Marian, V., Chabal, S., Bartolotti, J., Bradley, K., & Hernandez, A. E. (2014). Differential recruitment of executive control regions during phonological competition in monolinguals and bilinguals. *Brain and Language*, 139, 108–117.  
<https://doi.org/10.1016/j.bandl.2014.10.005>
- Mattis, S. (1988). *Dementia rating scale: professional manual*.
- Mechelli, A., Josephs, O., Lambon Ralph, M. A., McClelland, J. L., & Price, C. J. (2007). Dissociating stimulus-driven semantic and phonological effect during reading and naming. *Human Brain Mapping*, 28(3), 205–217. <https://doi.org/10.1002/hbm.20272>
- Minicucci, D., Guediche, S., & Blumstein, S. E. (2013). An fMRI examination of the effects of acoustic-phonetic and lexical competition on access to the lexical-semantic network. *Neuropsychologia*, 51(10), 1980–1988.  
<https://doi.org/10.1016/j.neuropsychologia.2013.06.016>
- Mirman, D., & Graziano, K. M. (2013). The Neural Basis of Inhibitory Effects of Semantic and Phonological Neighbors in Spoken Word Production. *Journal of Cognitive Neuroscience*, 25(9), 1504–1516. [https://doi.org/10.1162/jocn\\_a\\_00408](https://doi.org/10.1162/jocn_a_00408)
- Noonan, K. A., Jefferies, E., Corbett, F., & Lambon Ralph, M. A. (2010). Elucidating the nature of deregulated semantic cognition in semantic aphasia: Evidence for the roles of prefrontal and temporo-parietal cortices. *Journal of Cognitive Neuroscience*, 22(7), 1597–1613. <https://doi.org/10.1162/jocn.2009.21289>
- Noonan, K. A., Jefferies, E., Visser, M., & Lambon Ralph, M. A. (2013). Going beyond inferior prefrontal involvement in semantic control: evidence for the additional contribution of dorsal angular gyrus and posterior middle temporal cortex. *Journal of Cognitive Neuroscience*, 25(11), 1824–1850. [https://doi.org/10.1162/jocn\\_a\\_00442](https://doi.org/10.1162/jocn_a_00442)
- Nozari, N., & Pinet, S. (2020). A critical review of the behavioral, neuroimaging, and electrophysiological studies of co-activation of representations during word production. In *Journal of Neurolinguistics* (Vol. 53, p. 100875). Elsevier Ltd.  
<https://doi.org/10.1016/j.jneuroling.2019.100875>
- Olszowy, W., Aston, J., Rua, C., & Williams, G. B. (2019). Accurate autocorrelation modeling substantially improves fMRI reliability. *Nature Communications*, 10(1).  
<https://doi.org/10.1038/s41467-019-09230-w>
- Peramunage, D., Blumstein, S. E., Myers, E. B., Goldrick, M., & Baese-Berk, M. (2011). Phonological neighborhood effects in spoken word production: An fMRI study. *Journal of Cognitive Neuroscience*, 23(3), 593–603. <https://doi.org/10.1162/jocn.2010.21489>
- Poldrack, R. A., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1999). Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *NeuroImage*, 10(1), 15–35.  
<https://doi.org/10.1006/nimg.1999.0441>
- Ralph, M. A. L., Jefferies, E., Patterson, K., & Rogers, T. T. (2016). The neural and computational bases of semantic cognition. *Nature Reviews Neuroscience*, 18(1), 42–55.  
<https://doi.org/10.1038/nrn.2016.150>
- Righi, G., Blumstein, S. E., Mertus, J., & Worden, M. S. (2010). Neural systems underlying

- lexical competition: An eye tracking and fMRI study. *Journal of Cognitive Neuroscience*, 22(2), 213–224. <https://doi.org/10.1162/jocn.2009.21200>
- 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. <https://doi.org/10.1162/089892903322598120>
- Rodd, J. M., Davis, M. H., & Johnsrude, I. S. (2005). The Neural Mechanisms of Speech Comprehension: fMRI studies of Semantic Ambiguity. *Cerebral Cortex*, 15(8), 1261–1269. <https://doi.org/10.1093/cercor/bhi009>
- Roelofs, A. (1999). Phonological segments and features as planning units in speech production. *Language and Cognitive Processes*, 14(2), 173–200. <https://doi.org/10.1080/016909699386338>
- Sabri, M., Binder, J. R., Desai, R., Medler, D. A., Leitl, M. D., & Liebenthal, E. (2008). Attentional and linguistic interactions in speech perception. *NeuroImage*, 39(3), 1444–1456. <https://doi.org/10.1016/j.neuroimage.2007.09.052>
- Sahib, A. K., Mathiak, K., Erb, M., Elshahabi, A., Klamer, S., Scheffler, K., Focke, N. K., & Ethofer, T. (2016). Effect of temporal resolution and serial autocorrelations in event-related functional MRI. *Magnetic Resonance in Medicine*, 76(6), 1805–1813. <https://doi.org/10.1002/mrm.26073>
- Salthouse, T. A. (2009). When does age-related cognitive decline begin? *Neurobiology of Aging*, 30(4), 507–514. <https://doi.org/10.1016/j.neurobiolaging.2008.09.023>
- Schnur, T. T., Schwartz, M. F., Kimberg, D. Y., Hirshorn, E., Coslett, H. B., & Thompson-Schill, S. L. (2009). Localizing interference during naming: Convergent neuroimaging and neuropsychological evidence for the function of Broca's area. *Proceedings of the National Academy of Sciences of the United States of America*, 106(1), 322–327. <https://doi.org/10.1073/pnas.0805874106>
- Schriefers, H., Meyer, A. S., & Levelt, W. J. M. (1990). Exploring the time course of lexical access in language production: Picture-word interference studies. *Journal of Memory and Language*, 29(1), 86–102. [https://doi.org/10.1016/0749-596X\(90\)90011-N](https://doi.org/10.1016/0749-596X(90)90011-N)
- Schrouff, J., Kussé, C., Wehenkel, L., Maquet, P., & Phillips, C. (2012). Decoding Semi-Constrained Brain Activity from fMRI Using Support Vector Machines and Gaussian Processes. *PLoS ONE*, 7(4), e35860. <https://doi.org/10.1371/journal.pone.0035860>
- Schrouff, J., Rosa, M. J., Rondina, J. M., Marquand, A. F., Chu, C., Ashburner, J., Phillips, C., Richiardi, J., & Mourão-Miranda, J. (2013). PRoNTTo: pattern recognition for neuroimaging toolbox. *Neuroinformatics*, 11(3), 319–337.
- Seghier, M. L., Fagan, E., & Price, C. J. (2010). Functional subdivisions in the left angular gyrus where the semantic system meets and diverges from the default network. *Journal of Neuroscience*, 30(50), 16809–16817. <https://doi.org/10.1523/JNEUROSCI.3377-10.2010>
- Snijders, T. M., Vosse, T., Kempen, G., Van Berkum, J. J. A., Petersson, K. M., & Hagoort, P. (2009). Retrieval and Unification of Syntactic Structure in Sentence Comprehension: an fMRI Study Using Word-Category Ambiguity. *Cerebral Cortex*, 19(7), 1493–1503. <https://doi.org/10.1093/cercor/bhn187>
- Snyder, H. R., Feigenson, K., & Thompson-Schill, S. L. (2007). Prefrontal cortical response

- to conflict during semantic and phonological tasks. *Journal of Cognitive Neuroscience*, 19(5), 761–775. <https://doi.org/10.1162/jocn.2007.19.5.761>
- Soni, M., Lambon Ralph, M. A., Noonan, K., Ehsan, S., Hodgson, C., & Woollams, A. M. (2009). “L” is for tiger: Effects of phonological (mis)cueing on picture naming in semantic aphasia. *Journal of Neurolinguistics*, 22(6), 538–547. <https://doi.org/10.1016/j.jneuroling.2009.06.002>
- Swick, D., Ashley, V., & Turken, A. U. (2008). Left inferior frontal gyrus is critical for response inhibition. *BMC Neuroscience*, 9(1), 102. <https://doi.org/10.1186/1471-2202-9-102>
- Teige, C., Cornelissen, P. L., Mollo, G., Gonzalez Alam, T. R. del J., McCarty, K., Smallwood, J., & Jefferies, E. (2019). Dissociations in semantic cognition: Oscillatory evidence for opposing effects of semantic control and type of semantic relation in anterior and posterior temporal cortex. *Cortex*, 120, 308–325. <https://doi.org/10.1016/j.cortex.2019.07.002>
- Thompson-Schill, S. L., Aguirre, G. K., D’Esposito, M., & Farah, M. J. (1999). A neural basis for category and modality specificity of semantic knowledge. *Neuropsychologia*, 37(6), 671–676. [https://doi.org/10.1016/S0028-3932\(98\)00126-2](https://doi.org/10.1016/S0028-3932(98)00126-2)
- Thompson-Schill, S. L., Jonides, J., Marshuetz, C., Smith, E. E., D’Esposito, M., Kan, I. P., Knight, R. T., & Swick, D. (2002). Effects of frontal lobe damage on interference effects in working memory. *Cognitive, Affective and Behavioral Neuroscience*, 2(2), 109–120. <https://doi.org/10.3758/CABN.2.2.109>
- Thompson, H. E., Almaghyuli, A., Noonan, K. A., Barak, O., Lambon Ralph, M. A., & Jefferies, E. (2018). The contribution of executive control to semantic cognition: Convergent evidence from semantic aphasia and executive dysfunction. *Journal of Neuropsychology*, 12(2), 312–340. <https://doi.org/10.1111/jnp.12142>
- Thompson, H. E., Robson, H., Lambon Ralph, M. A., & Jefferies, E. (2015). Varieties of semantic “access” deficit in Wernicke’s aphasia and semantic aphasia. *Brain*, 138(12), 3776–3792. <https://doi.org/10.1093/brain/awv281>
- Tun, P. A., O’Kane, G., & Wingfield, A. (2002). Distraction by competing speech in young and older adult listeners. *Psychology and Aging*, 17(3), 453–467. <https://doi.org/10.1037/0882-7974.17.3.453>
- Vigneau, M., Beaucousin, V., Hervé, P. Y., Duffau, H., Crivello, F., Houdé, O., Mazoyer, B., & Tzourio-Mazoyer, N. (2006). Meta-analyzing left hemisphere language areas: Phonology, semantics, and sentence processing. *NeuroImage*, 30(4), 1414–1432. <https://doi.org/10.1016/j.neuroimage.2005.11.002>
- Visser, M., Jefferies, E., Embleton, K. V., & Ralph, M. A. L. (2012). Both the middle temporal gyrus and the ventral anterior temporal area are crucial for multimodal semantic processing: Distortion-corrected fMRI evidence for a double gradient of information convergence in the temporal lobes. *Journal of Cognitive Neuroscience*, 24(8), 1766–1778. [https://doi.org/10.1162/jocn\\_a\\_00244](https://doi.org/10.1162/jocn_a_00244)
- Wagenmakers, E.-J. (2007). A practical solution to the pervasive problems of p values. *Psychonomic Bulletin and Review*, 14(5), 779–804. <https://doi.org/10.3758/BF03194105>
- Wagner, A. D., Paré-Blagoev, E. J., Clark, J., & Poldrack, R. A. (2001). Recovering meaning:

- Left prefrontal cortex guides controlled semantic retrieval. *Neuron*, 31(2), 329–338.  
[https://doi.org/10.1016/S0896-6273\(01\)00359-2](https://doi.org/10.1016/S0896-6273(01)00359-2)
- Wang, M., Shao, Z., Chen, Y., & Schiller, N. O. (2018). Neural correlates of spoken word production in semantic and phonological blocked cyclic naming. *Language, Cognition and Neuroscience*, 33(5), 575–586. <https://doi.org/10.1080/23273798.2017.1395467>
- Whitney, C., Kirk, M., O’Sullivan, J., Lambon Ralph, M. A., & Jefferies, E. (2011). The Neural Organization of Semantic Control: TMS Evidence for a Distributed Network in Left Inferior Frontal and Posterior Middle Temporal Gyrus. *Cerebral Cortex*, 21(5), 1066–1075. <https://doi.org/10.1093/cercor/bhq180>
- Xie, X., & Myers, E. (2018). Left inferior frontal gyrus sensitivity to phonetic competition in receptive language processing: A comparison of clear and conversational speech. *Journal of Cognitive Neuroscience*, 30(3), 267–280.  
[https://doi.org/10.1162/jocn\\_a\\_01208](https://doi.org/10.1162/jocn_a_01208)