Controlled retrieval relies on directed interactions between semantic control regions and visual cortex: MEG evidence from oscillatory dynamics

Abbreviated Title: Directed connectivity underpins semantic control

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Abstract

To navigate the world, we store knowledge about relationships between concepts and retrieve this information flexibly to suit our goals. The semantic control network, comprising left inferior frontal gyrus (IFG) and posterior middle temporal gyrus (pMTG), is thought to orchestrate this flexible retrieval by modulating sensory inputs. However, interactions between semantic control and input regions are not sufficiently understood. Moreover, pMTG's well-formed structural connections to both IFG and visual cortex suggest it as a candidate region to integrate control and input processes. We used magnetoencephalography to investigate oscillatory dynamics during semantic decisions to pairs of words, when participants did or did not know the type of semantic relation between them. IFG showed early increases and decreases in oscillatory activity to prior task knowledge, while pMTG only showed positive effects of task knowledge at a later time window. Furthermore, both regions provided feedback to visual cortex when task goals were absent, while IFG also provided feedback when goals were known. This goal-dependent feedback coincided with an earlier onset of feedforward signalling from visual cortex to pMTG, indicating rapid retrieval of task-relevant features. Knowledge of task goals also enhanced simultaneous inputs to pMTG from both IFG and visual cortex, consistent with the view that pMTG integrates top-down control with bottom-up input. Our findings elucidate the separate roles of anterior and posterior components of the semantic control network and reveal the spectro-temporal cascade of interactions between semantic control and visual regions that underlie our ability to flexibly adapt cognition to the current goals.

Significance Statement

Using magnetoencephalography, we characterize the spectro-temporal dynamics that underlie our ability to flexibly adapt semantic cognition to the current context and goals. We find that semantic goals increase oscillatory activity first in IFG and later in pMTG, and ultimately facilitate visual processing. Effective connectivity analyses confirm the proposed direct modulation of visual cortex by semantic control regions both in the presence and absence of goals, resulting in rapid retrieval when semantic goals are known. Moreover, our findings suggest differential roles for the two semantic control regions: while IFG *controls* early goal-dependent retrieval, pMTG *integrates* top-down information from IFG with bottom-up visual input later.

1 Introduction

Our semantic memory is thought to draw on multimodal abstraction across experiences to extract knowledge about objects, words, and their relations, which we flexibly retrieve to suit the circumstances (Lambon Ralph et al., 2017). For example, to prepare a fruit pie, we exploit *thematic* knowledge that apples are used as a pie filling and locate the relevant aisle in the supermarket by retrieving *taxonomic* knowledge that apples are fruit. Semantic control implemented within the left inferior frontal gyrus (IFG) and posterior middle temporal gyrus (pMTG; Noonan et al., 2013; Jackson, 2021) is thought to support this ability to flexibly adapt semantic retrieval to suit our goals (Jefferies, 2013). Previous functional magnetic resonance imaging (fMRI) studies mainly implicated these brain regions in demanding semantic cognition, such as when two words are weakly as opposed to strongly related (Gao et al., 2021; Jackson, 2021). In contrast, fewer studies focused on the role of these regions when the semantic context (Grindrod et al., 2008) or the goal for retrieval (Zhang et al., 2021) is known in advance, facilitating semantic cognition. Zhang et al. (2021) investigated the ability to flexibly exploit taxonomic or thematic knowledge based on our goals, using fMRI. Participants decided if two sequentially presented words were related, and on half the trials a preceding cue revealed whether the upcoming words would share a taxonomic or thematic relation. Knowledge of the relation increased activation in IFG, indicating its role in goal-dependent semantic cognition. In addition, an interaction between this task knowledge and the presentation order of the words emerged in visual cortex: activation was stronger to the first word when the retrieval goal was known, and stronger to the second word when the goal was unknown (Zhang et al., 2021). This suggests that semantic goals enable an earlier onset of visual processing, potentially through the gating of input processes within unimodal ‘spokes’ (i.e., modality-specific input regions; Jackson et al., 2021).

However, the relative timing and directed interactions of these goal-dependent effects in IFG and visual cortex cannot easily be inferred from fMRI findings. Consequently, it remains unclear whether cortical regions supporting semantic control play a direct, early role in the gating of visual activation during goal-dependent cognition. While top-down connections from frontal to occipital cortex are implicated in word reading (Schurz et al., 2014; Woodhead et al., 2014), object (Bar et al., 2006), and face recognition (Karimi-Rouzbahani et al., 2021), it is unclear whether prior semantic knowledge modifies such connections. Furthermore, computational modelling indicated the need of a region that integrates bottom-up input with controlled top-down processes in semantic cognition (Giallanza et al. 2004). pMTG is a candidate for such a process since it is well connected anatomically to both visual cortex and IFG (Turken and Dronkers, 2011). Directional time-resolved connectivity measures can address these issues and confirm whether pMTG receives both top-down input from IFG and bottom-up input from visual cortex.

Here, we used magnetoencephalography (MEG) to investigate the spectro-temporal dynamics and directional connectivity between semantic control regions and visual cortex during goal-oriented semantic cognition. We used Zhang et al.'s paradigm (2021), in which participants either knew or did not know whether a subsequent semantic judgement would be based on a taxonomic or thematic link. In time-frequency space, we asked whether effects of task knowledge in semantic control regions (IFG and pMTG) precede interactions of task knowledge with bottom-up input in visual cortex (Fig. 1a). We then used spectral Granger Causality to investigate the effective connectivity between semantic control regions and visual cortex. If interactions between task goals and visual processes are driven by semantic control regions, top-down effects should precede or coincide with bottom-up inputs (Fig. 1b). Finally, we delineated the role of pMTG by investigating whether it provides top-down constraint over

visual cortex or integrates top-down influences from IFG with bottom-up inputs (Fig. 1c). In this way we elucidate the architecture of controlled semantic retrieval over time and frequency.

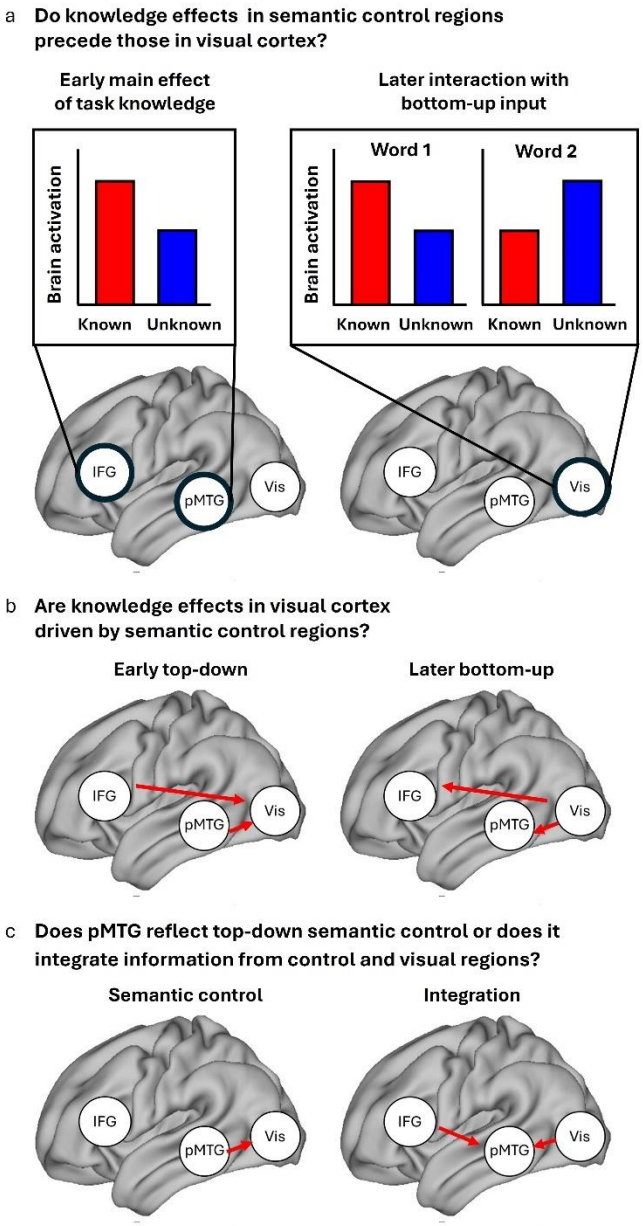


Figure 1. Research questions and predictions: **a)** Higher brain activation in semantic control regions (left IFG and pMTG) for known vs. unknown semantic goals (left) is expected to precede interactions between task knowledge and word order in visual cortex (right). For the interaction in visual cortex, we expect that during the presentation of the first word, brain activation is higher in the known goal condition while for the second word, activation is higher in the unknown goal condition (Zhang et al., 2021). The use of MEG allows us to disentangle the extent to which these effects occur in different time windows and frequency bands. **b)** If task knowledge effects in visual cortex are driven by semantic control regions, we expect to observe an early top-down connection from semantic control regions to visual cortex in the known condition (left), which precedes or coincides with the bottom-up connection in the reverse direction (right). **c)** Connectivity patterns can further discriminate the functional role of left pMTG: If this region is predominantly involved in semantic control (cf. Jackson, 2021), we expect to observe top-down connections from this region to visual cortex (left). However, if pMTG (additionally) serves the integration of task knowledge and bottom-up input, it should receive inputs from both semantic control regions (IFG) and visual cortex (right).

2 Methods

2.1 Participants

Behavioural study

In order to investigate the effect of top-down goals on semantic decisions, a behavioural study examined the performance of 20 participants (18 females, mean age 20.7±2.9 years, range 18-29 years; 16 right-handed) who did not complete the neuroimaging investigation, using a version of the task in which responses were made on each trial. This behavioural study was included since in the MEG version, participants were instructed to only respond to unrelated catch trials, in order to prevent contamination of the related trials from motoric activation. In addition, we selected word pairs for the MEG study based on the behavioural results (see section 2.2). Participants were native English speakers and did not have any language disorders or psychiatric conditions. A further five participants were excluded due to insufficient task performance (i.e., below 50% correct responses, N = 4) or not meeting the inclusion criteria (N = 1). Participants gave informed consent before participation and received a voucher or course credit as compensation. The study was approved by the ethics committee of the Department of Psychology, University of York.

MEG study

Twenty-eight participants (21 females, mean age 20.2 years, range 18-27 years) completed the MEG study and were entered into final data analysis. Participants were right-handed native English speakers with (corrected-to-) normal vision and did not have any language disorder or psychiatric condition. Of the original sample of 35 participants, seven were excluded due to poor task performance (N = 1, only 60% of unrelated trials detected), insufficient number of trials (<40 per condition) after artifact rejection (N = 5) and not completing the experiment (N = 1). Participants gave informed consent before participation and received vouchers or course

credit as compensation. The study was approved by the ethics committee of York Neuroimaging Centre, University of York.

2.2 Stimulus materials

A total of 392 word pairs were presented in a behavioural semantic priming study, including stimuli from Teige et al. (2019) and Zhang et al. (2021). 153 word pairs were categorically related, for example, both words could be birds (peacock - penguin) or vehicles (bicycle - lorry). 179 word pairs were thematically related, i.e., the two items frequently occurred in the same context (e.g., coral - diver or armchair - fireplace). Sixty word pairs were unrelated. Categorical word pairs were not thematically related and vice versa, as indicated from ratings by a different sample of 30 participants. These ratings confirmed that categorical word pairs were more visually similar than thematic word pairs. Based on the behavioural results, we selected a subset of 120 categorically related, 120 thematically related and 60 unrelated word pairs for the MEG study which were responded to correctly by the majority of participants in the behavioural study (82.9% on average; range: 40-100%). In this subset, prime and target words as well as words from categorical and thematic pairs were matched for word length, word frequency and imageability using 'Match' (van Casteren and Davis, 2007). Stimulus characteristics are presented in Table 1.

2.3 Experimental procedure and task

The behavioural study was carried out online using the Gorilla Experiment Builder (www.gorilla.sc; Anwyl-Irvine, et al., 2020). Words were presented in black in front of a white background (Fig. 2). The procedure followed that of Zhang et al. (2021) with shorter presentation durations. Each trial started with the presentation of two vertical black bars (nonius lines) indicating the center of the screen where participants were asked to fixate.

Nonius lines were presented for a jittered duration between 800 and 1800 ms. Then, a cue which either read ‘Category?’, ‘Thematic?’, or ‘Them/Cat?’ was presented for 600 ms. In known goal trials, word pairs were from the same category or thematically related, and preceded by the respective cue (‘Category’ and ‘Thematic’, respectively). In unknown goal trials, word pairs that were from the same category or thematically related were preceded by an unspecific cue (‘Them/Cat?’). Unrelated word pairs could either be preceded by the unspecific cue (50%) or either of the specific cues (25% each). After a 600 ms delay following cue presentation, prime and target word were presented in sequential order for 600 ms each, separated by a delay period of 600 ms. The nonius lines stayed on screen throughout cue, prime and target presentation, as well as the delay periods. At the end of each trial, nonius lines were presented for 900 ms, followed by a blank screen of 1200 ms. Trials were presented in pseudo-random order, such that transition probabilities between conditions were equal. Participants were instructed to respond as quickly and accurately as possible by pressing a key with their left or right index finger whether prime and target word were semantically related or unrelated.

At the beginning of the study, participants were informed about the difference between taxonomic and thematic relations and performed a short training procedure of four trials in which they had to respond by button press if two simultaneously presented words shared a taxonomic or thematic relation and received feedback on every trial. Then, they completed a practice run of the main task including twelve trials with feedback on total accuracy presented at the end. If necessary, each training procedure was repeated until an accuracy of at least 75 % was reached. Trials from the training procedures were not used in the main experiment. After a subset of the behavioural data had been collected, we slightly changed the instruction at the start of the experiment: Participants were now explicitly informed that they would be presented with a higher number of related than unrelated word pairs. Of our included sample, nine participants were informed about this while eleven were not.

For the MEG study, stimuli were presented using Psychopy (version 3.1.5; Peirce et al., 2019) and projected onto a screen at a distance of ca. 90 cm of the participants. A neutral density filter was used to reduce glare. Presentation durations were identical to the behavioural study. Participants were instructed to respond as quickly and accurately as possible by pressing a key with their left or right index finger only when prime and target word were not semantically related. This approach prevented contamination of the MEG signal during related trials with the motor response. Response hands were counterbalanced across participants. Trials involving button presses were excluded from MEG data analysis. The MEG study was divided into four runs. Prior to the first run, participants completed a practice run of 25 trials with feedback on overall accuracy presented at the end. Training was repeated if the accuracy was less than 75 %. Participants were informed at the start of the experiment that there would be a higher number of related than unrelated word pairs. On the day before the MEG study, participants were informed about the difference between taxonomic and thematic relations via an online Zoom meeting, which was reiterated on the day of the MEG study.

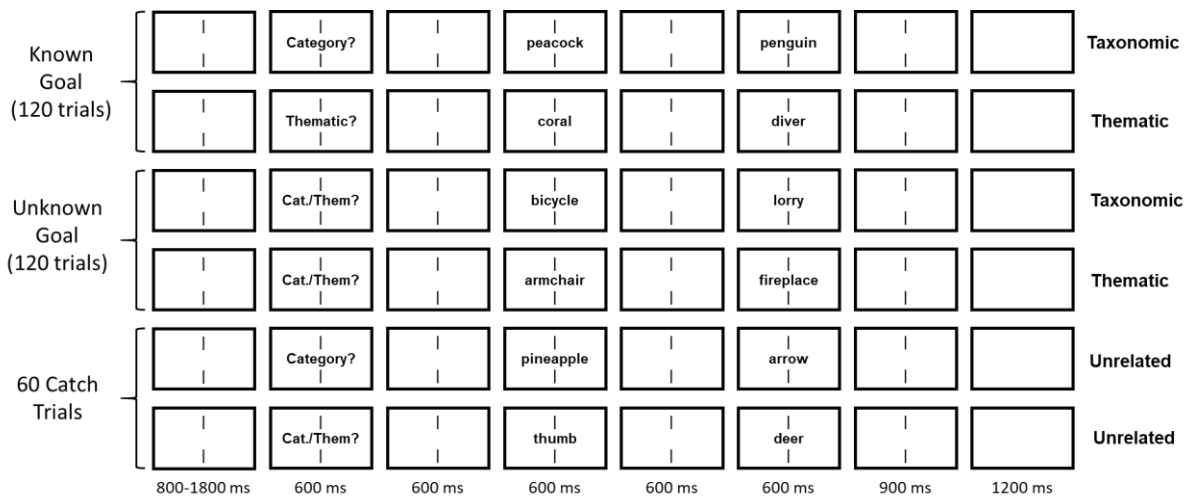


Figure 2. Experimental procedure. Each trial started with the presentation of nonius lines for a jittered interval between 800 and 1800 ms, followed by the presentation of a cue, a prime and a target stimulus for 600 ms each, separated by intervals of 600 ms. The nonius lines remained on screen the entire time, including a 900 ms interval following target offset, after which a blank screen was presented for

1200 ms. Prime and target could be taxonomically related, thematically related, or unrelated. Half of the taxonomically and thematically related trials were known goal trials, i.e., the cue indicated if they were taxonomically ('Category?') or thematically related ('Thematic'). The other half were unknown goal trials, which were preceded by an unspecific cue ('Them/Cat?').

2.4 Behavioural analysis

Statistical analyses of the behavioural study were performed using R, version 4.0.4, 2021-02-15 (R Development Core Team, 2008) and focused on the 240 semantically related trials selected for the MEG study. Log-transformed response times of correct responses were investigated in linear mixed models (LMMs) using the lmerTest package (Kuznetsova et al., 2017). For accuracies, we assumed a binary distribution for the outcome and therefore used generalized linear mixed models (GLMMs) with a logit link function. (G)LMMs included the fixed effects of task knowledge (known vs. unknown goal) and its two-way interactions with semantic relation (taxonomic vs. thematic) and semantic similarity (based on word2vec). The main models controlled for fixed effects of trial order and instruction (after the first 11 included participants, the instruction explicitly informed participants that there would be more related than unrelated word pairs), as well as random effects of participant, prime, and target. In addition, more complex models also controlled for fixed effects of the prime's and target's word length, word frequency, and imageability. Fixed effects were reduced in a step-wise procedure based on Akaike information criterion. For visualization of partial effects in the response time analysis, we used the remef package (Hohenstein & Kliegl, 2015).

2.5 MEG data acquisition

MEG data were acquired using a 248-sensor Magnes3600 system (4-D Neuroimaging, San Diego, California) at a sampling frequency of 2,000 Hz. Five sensors were disabled or excluded from analysis due to technical issues. External noise detected by the MEG reference channels

was removed from the data. Five head localization coils recorded participants' head positions relative to the sensor array at the beginning and end of each experimental run. Coil positions and participants' head shapes were recorded with a 3D digitizer (Fastrak Polhemus) before MEG data acquisition to improve co-registration with the anatomical magnetic resonance (MR) images. For one participant, the recorded head shape was not saved due to technical issues. In this case, co-registration was based on landmarks (nasion, left and right pre-auricular points) identified from the anatomical MR image.

2.6 Structural MR image acquisition

Structural T1-weighted MR images were acquired with a 3 Tesla Siemens Prisma scanner (Siemens Medical Systems) using a 3D MPRAGE sequence (176 slices, 1x1x1 mm voxel size, 2.3 s TR, 2.26 s TE, 8° flip angle).

2.7 MEG preprocessing

The MEG data analysis focused on related word pairs. MEG data were preprocessed using FieldTrip (Version 06/2021; http://fieldtrip.fcdonders.nl; Oostenveld et al., 2011) under MATLAB (version 2019a, The MathWorks Inc., Natick, MA). MEG data were segmented into epochs containing a 700 ms baseline and the time windows of cue, prime, and target presentation, plus an additional 380 ms after target offset to allow for sufficient data for time-frequency analysis. Thus, epochs were lasting from −700 ms to 2,180 ms with respect to cue onset. 50 Hz line noise was removed using a discrete Fourier transform filter. Trials which included button presses at any time point from –700 ms until the onset of the next trial were excluded from analysis. In addition, trials which included sensor jump, muscle, or eye movement artifacts in the time period from −700 ms to 2,180 ms were excluded from analysis. Trials with artifacts in the baseline time window were excluded completely, while trials that

only contained artifacts in the prime but not target presentation time window and vice versa were only excluded from analysis of the respective time window. Artifacts were identified using the standard FieldTrip routine for automatic artifact detection. Filters applied to the data prior to artifact detection were a 9th order median filter for jump artifacts, a 7th order Butterworth IIR filter (110-140 Hz) for muscle artifacts, and a 3rd order Butterworth IIR filter (2-15 Hz) for eye movement artifacts. Eye movement artifact detection was based on nine frontal sensors, while muscle and jump artifact detection took all sensors into account. The filtered data were *z*-transformed and averaged across sensors. Trials were rejected if, for any time point, the z-value exceeded a threshold of z = 40 for jump artifacts, z = 30 for muscle artifacts, and z = 10 for eye movement artifacts. A visual inspection confirmed this procedure was sufficient to remove artifacts. 85 trials on average per participant and condition were retained for further analyses (range: 41 to 110).

2.8 MEG source localization

Source localization was performed separately for the first half (runs 1 and 2) and second half (runs 3 and 4) of the experiment, in order to minimize the effects of participants' head movements over the course of the experiment. On average, the median difference in head position from the beginning of the first to the beginning of the third run or from the beginning of the third to the end of the fourth run across participants was 8 mm (range: 0.8 to 34.4 mm). Source localization was performed at the single-trial level using linearly constrained minimum variance (LCMV) spatial filters (Van Veen et al., 1997). The data covariance matrix was estimated based on all trials. Forward models were based on T1-weighted images co-registered and warped to an MNI-space template that comprised 1,619 voxels within the brain at 10 mm resolution. A single shell forward model of the inner surface of the skull (Nolte, 2003) was used for lead field computation. Spatial filters were computed based on the optimal dipole

orientation that maximized spatial filter output, which was identified using singular value decomposition. Single-trial source power based on the precomputed spatial filters was then estimated for each voxel location.

2.9 Time-frequency analysis

Time-frequency analysis focused on total oscillatory power between 4 and 50 Hz, i.e., the theta to low-gamma range, which is sensitive to meaning-based contexts (Prystauka and Lewis, 2019), semantic task manipulations (Rahimi et al., 2022), and the strength of the association between words (Teige et al., 2018; 2019). A time-frequency transformation was performed on source power estimates using a Hanning taper with three cycles per time window, a frequency resolution of 1 Hz and a temporal resolution of 25 ms. A relative baseline correction using the time interval from -300 to -25 ms before the onset of the cue was performed. For each participant and condition, time-frequency estimates were averaged across trials and the two halves of the experiment in three regions of interest (ROIs): Based on the fMRI study by Zhang et al. (2021), the left IFG cluster showing a task knowledge effect, as well as the bilateral visual cortex cluster showing an interaction between task knowledge and word order were selected as ROIs. In addition, we selected the left pMTG cluster (which peaks in pMTG and posterior inferior temporal gyrus) implicated in semantic control from a recent fMRI meta-analysis (Jackson, 2021). These sites were selected to investigate the relationship between anterior and posterior nodes of the semantic control network (left IFG vs. pMTG) and the interaction of these regions with visual cortex in different phases of the paradigm, when the nature of the semantic relationship was known in advance or not.

In each ROI, time-frequency power estimates were compared between conditions using cluster-based permutation tests (Maris and Oostenveld, 2007) for dependent samples, corrected for multiple comparisons across time points (0 to 600 ms) and frequencies (4 to 50 Hz) at

cluster level. One analysis included the 2x2 interaction between task knowledge (known vs. unknown) and word order (word 1 vs. 2), using the permANOVA function by Helbling (2015; https://github.com/sashel/permANOVA/) combined with Fieldtrip (version 20130106). A separate analysis, focused on the presentation time window of the second word, investigated the binary effects of high versus low semantic similarity (word2vec) based on a median split. For this analysis, the ten percent of trials closest to the median, identified separately for each knowledge condition and participant, were excluded from analysis. Clusters were defined as spectrally and temporally adjacent samples with F- or t-values exceeding an uncorrected α-level of 0.05 (0.025 at each tail in the case of t-values). The cluster-level statistic was calculated using the standard approach, i.e., taking the sum of F- or t-values within a cluster (Maris and Oostenveld, 2007). Empirical cluster-level statistics were compared to the distribution of cluster-level statistics obtained from Monte Carlo simulations with 1,000 permutations, in which condition labels were randomly exchanged within each participant. Original cluster-level statistics larger than the 95th percentile of the distribution of cluster-level statistics obtained in the permutation procedure were considered significant.

2.10 Spectral Granger Causality

Source power estimates were baseline corrected by subtracting the power from the interval between -300 to 0 ms before the onset of the cue. A fast Fourier transform between 0 and 100 Hz was performed on source power estimates using multitapers with a frequency resolution of 3.3 Hz for three overlapping time windows of interest: 0 to 300 ms, 150 to 450 ms, and 450 to 600 ms (see Schaum et al., 2021, for a similar approach). Spectral Granger Causality (Granger, 1969; Geweke, 1982) was used to assess the direction of information flow between ROIs. This method reveals a directed connection from brain region X to brain region Y if the prediction of the present time series of Y based on its past time series can be improved by adding the past

time series of X (Dhamala et al., 2008). The spectral Granger Causality analysis was performed on the single-trial Fourier transformed data combined across the two halves of the experiment for each pairwise combination of the three ROIs, obtaining feedforward and feedback spectral connectivity estimates per participant, condition, and time window.

For each combination of a pair of ROIs, a connectivity direction (feedforward or feedback), and a time window, the 2x2 interaction between task knowledge (known vs. unknown) and word order (word 1 vs. 2) was assessed using a cluster-based permutation test (Maris and Oostenveld, 2007) and the permANOVA function by Helbling (2015; https://github.com/sashel/permANOVA/) combined with Fieldtrip (version 20130106). In a separate analysis, we investigated the effect of semantic similarity (based on word2vec) on spectral Granger Causality estimates during the presentation of the second word, using the median-split approach as described for the time-frequency analysis. Multiple comparison correction across frequencies (4 to 50 Hz) was performed at the cluster level. Resulting p-values were then Bonferroni-corrected for the number of tests across ROI combinations, connectivity directions, and time windows (18 tests in total). Clusters were defined as spectrally adjacent samples with F- or t-values exceeding an uncorrected α-level of 0.05 (0.025 at each tail in the case of t-values). The cluster-level statistic was calculated by taking the sum of F-values within a cluster (Maris and Oostenveld, 2007). Empirical cluster-level statistics were compared to the distribution of cluster-level statistics obtained from Monte Carlo simulations with 5,000 permutations, in which condition labels were randomly exchanged within each participant. Original cluster-level statistics larger than the 95th percentile of the distribution of cluster-level statistics obtained in the permutation procedure were considered significant.

2.11 Code and Data Accessibility

All analysis code is publicly available at the Open Science Framework (https://osf.io/j9pz4/). The conditions of our ethics approval do not permit public archiving of the raw MEG and MRI data supporting this study. Readers seeking access to this data should contact the lead author, Susanne Eisenhauer, the PI Professor Beth Jefferies, or the local ethics committee at the Department of Psychology and York Neuroimaging Centre, University of York. Access will be granted to named individuals in accordance with ethical procedures governing the reuse of sensitive data. Specifically, the following conditions must be met to obtain access to the data: approval by the Department of Psychology and York Neuroimaging Research Ethics Committees and a suitable legal basis for the release of the data under GDPR.

3 Results

3.1 Behaviour

In the behavioural study, we found significant main effects of task knowledge and semantic similarity, reflecting faster responses when the semantic goal was known vs. unknown (Fig. 3a), as well as when the two words were more strongly linked (Fig. 3b; Table 2). The main effect of trial order also reached significance, indicating that response times increased throughout the experiment. There was no main effect of semantic relation (taxonomic vs. thematic) and no interactions between task knowledge and either semantic relation or semantic similarity. The same pattern of results was found in a more complex linear model (based on the subset of trials for which imageability ratings were available) that also controlled for the effects of prime and target word length, word frequency, and imageability (Table 3).

Concerning response accuracy, the simple general linear model revealed a significant interaction between task knowledge and semantic relation (Table 4). Accuracy was higher for known vs. unknown trials in thematic but not taxonomic word pairs (Fig. 3c). Moreover, accuracy was significantly higher for word pairs of increasing semantic similarity, irrespective of task knowledge (Fig. 3d). In the more complex linear model controlling for prime and target word characteristics (based on the subset of trials for which imageability ratings were available), a similar main effect of semantic similarity was found; however, the interaction between task knowledge and semantic relation, as well as the main effect of task knowledge, did not reach significance (Table 5). To sum up, the behavioural findings indicated that semantic relatedness decisions were facilitated both when semantic goals were known in advance, as well as when word pairs were more semantically similar.

In the MEG study, participants performed the task with high accuracy, correctly responding to 93.7% of unrelated trials, and correctly refraining from a response to 93.8% of known and 93.6% of unknown goal trials.

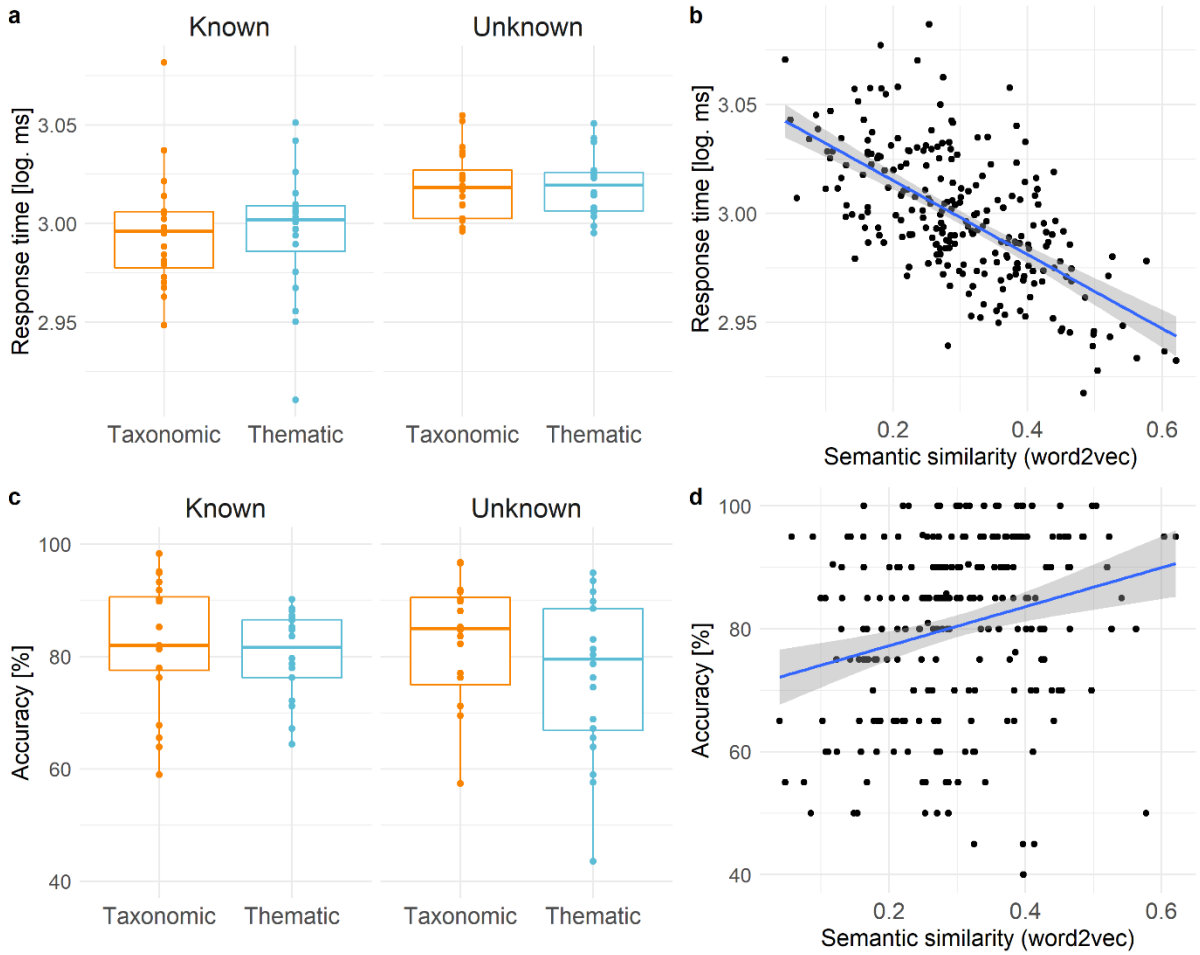


Figure 3. Response times and accuracy for each condition (a, c) as well effects of semantic similarity based on word2vec (b, d). In a and b, partial effects from linear mixed models are shown. Each dot represents a word averaged across participants.

3.2 Time-frequency representations

We investigated the interaction of task knowledge and word order, using cluster-based permutation tests in three ROIs: the left IFG, left pMTG, and bilateral visual cortex (Extended Data Figure 4-1). The presentation of the two words elicited synchronized oscillatory responses relative to the pre-cue baseline in all three ROIs (Extended Data Figure 4-1). Main effects of word order were found in all three ROIs and are shown in Extended Data Figure 4-2. Main effects of task knowledge and its interactions with word order are described below.

In left IFG, a main effect of task knowledge was found in two clusters (Fig. 4, top). In the theta/alpha band, relative power was higher in the known than in the unknown goal condition from ~100 to 350 ms. In the gamma band at 225 ms, the opposite pattern with higher power in the unknown than in the known goal condition was found.

In left pMTG, a main effect of task knowledge was found from ~200 to 500 ms, indicating higher power in the known than in the unknown goal condition in the theta band (Fig. 4, middle).

In bilateral visual cortex, main effects of task knowledge were found in two temporally adjacent clusters in the alpha/low beta range between 400 and 600 ms, indicating higher power in the unknown compared to the known goal condition (Fig 4, bottom). Furthermore, bilateral visual cortex showed interactions between task knowledge and word order in three clusters (Fig. 5). Within the first 200 ms, alpha/low beta power increased from the first to the second word, particularly within the unknown condition. In two clusters from ~450 to 600 ms, high alpha to low gamma power decreased from the first to the second word, and remained higher in the unknown than in the known condition. These two later clusters highly overlapped with the two clusters showing a main effect of task knowledge.

Furthermore, we investigated effects of the semantic similarity between the two related words in a trial, based on word2vec. Significant effects of semantic similarity were found in

pMTG from 350 to 550 ms (peaking at 425 ms, 12 Hz; Fig. 6, top), as well as in visual cortex from 0 to ~550 ms (peaking at 50 ms, 10 Hz; Fig. 6, bottom). In both regions, alpha/low beta power was higher for word pairs with lower semantic similarity.

To summarise our findings (Fig. 7), the earliest observed knowledge effects were increases in theta/alpha band activity in left IFG, peaking at 7 Hz and 200 ms after word onset (across both words). At a similar time (~225 ms), IFG gamma band activity (peaking at 33 Hz) showed the reverse pattern with higher power in the unknown goal condition. Knowledge effects were not observable in left pMTG until later. Around 350 ms post word onset, theta band activity in left pMTG (peaking at 6 Hz) resembled the pattern observed earlier in IFG, i.e., higher power in the known condition. Bilateral visual cortex only demonstrated significant knowledge effects for the second word. Here, greater power for the unknown goal condition was identified around stimulus onset, in alpha/beta frequencies (peaking at 10 Hz), and around 600 ms, within the beta band (peaking at 31 Hz). When participants made decisions about less similar word pairs, there was higher alpha/beta power in bilateral visual cortex extending throughout much of the trial after presentation of the second word. A similar pattern was found in the left pMTG, albeit in a later time window around 425 ms.

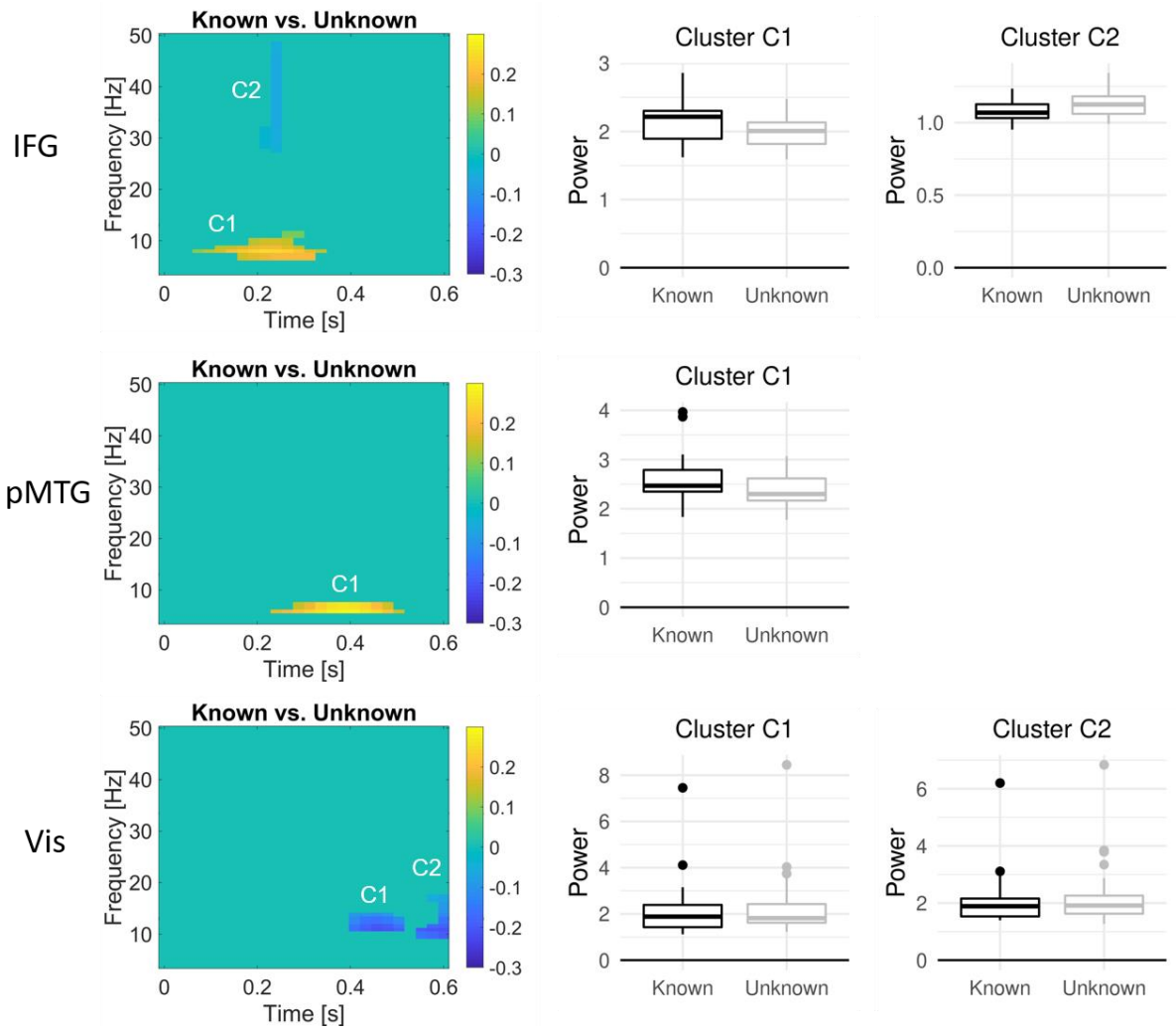
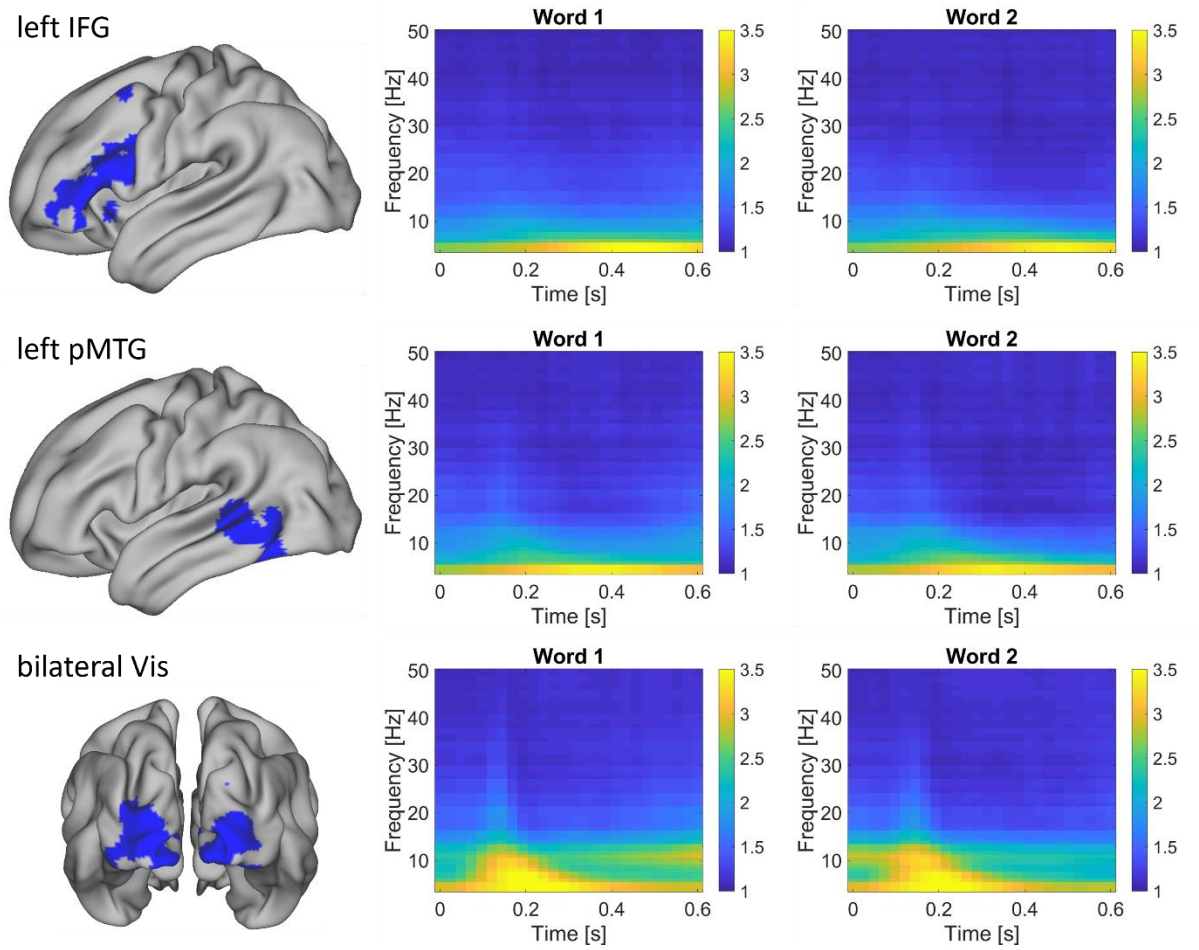
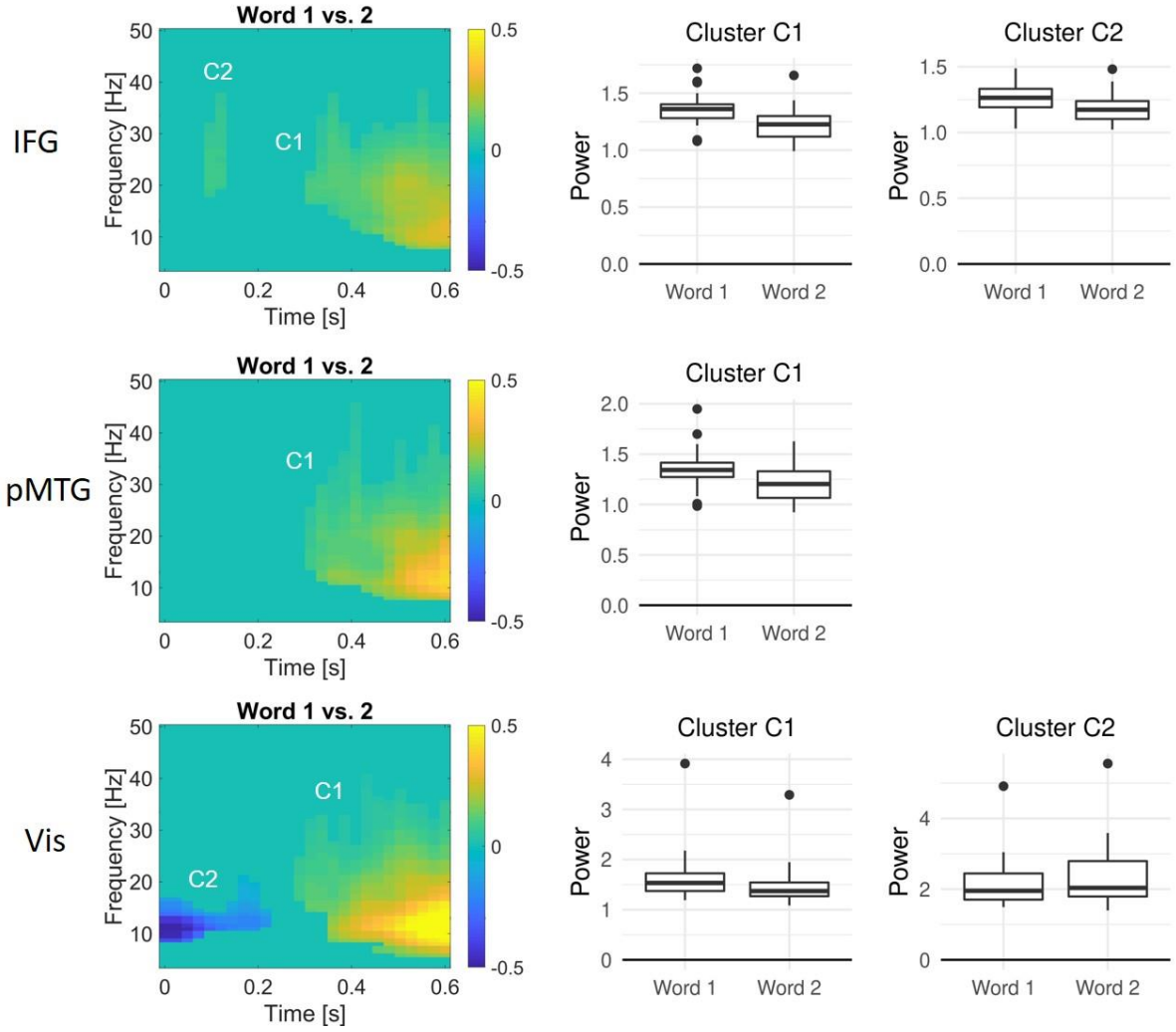


Figure 4. Oscillatory dynamics of the main effect of task knowledge in left IFG (top), left pMTG (middle), and bilateral visual cortex (bottom). Time-frequency plots show the difference between known and unknown trials, averaged across the first and second word, in significant clusters. Boxplots show the oscillatory power in each significant cluster for known and unknown trials across participants. Raw oscillatory responses to the first and second word are shown in Extended Data Figure 4-1. Main effects of word order are shown in Extended Data Figure 4-2.



Extended Data Figure 4-1. Brian regions of interest (left) and time-frequency representations of oscillatory power (middle, right), relative to the pre-cue baseline, in the left IFG (top), left pMTG (middle), and bilateral visual cortex (bottom) during the presentation of Word 1 and 2, averaged across knowledge conditions.



Extended Data Figure 4-2. Oscillatory dynamics of the main effect of word order in left IFG (top), left pMTG (middle), and bilateral visual cortex (bottom). Time-frequency plots show the difference between known and unknown trials, averaged across knowledge conditions, in significant clusters. Boxplots show the oscillatory power in each significant cluster for Word 1 and 2 across participants.

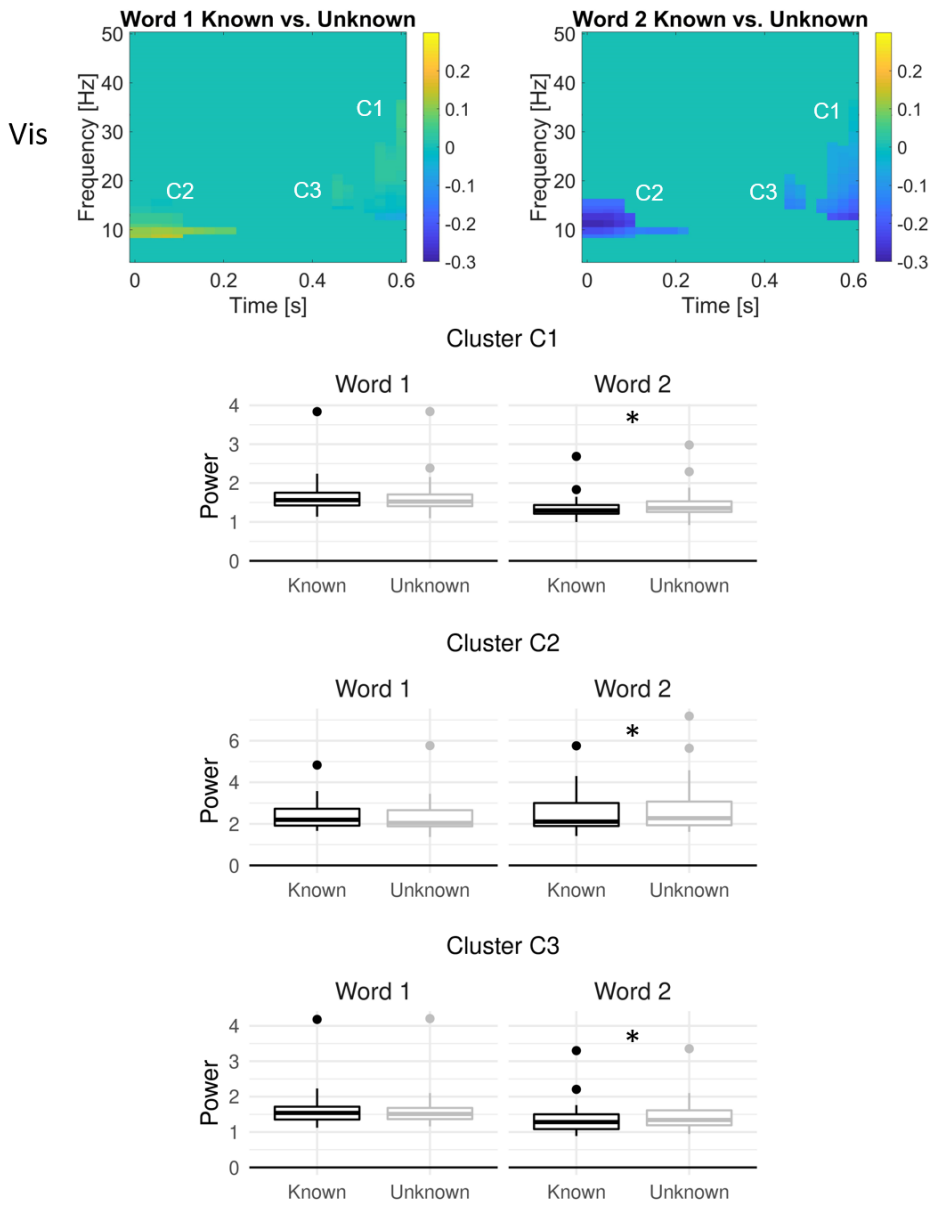


Figure 5. Oscillatory dynamics of the interaction between task knowledge and word order in bilateral visual cortex. Time-frequency plots show the difference between known and unknown trials for word 1 (left) and word 2 (right) in significant clusters. Boxplots show the oscillatory power in each significant cluster for known and unknown trials in word 1 and word 2 across participants. Asterisks indicate post-hoc significant differences between the known and unknown goal conditions at the second word only. No significant interactions were found for the other ROIs.

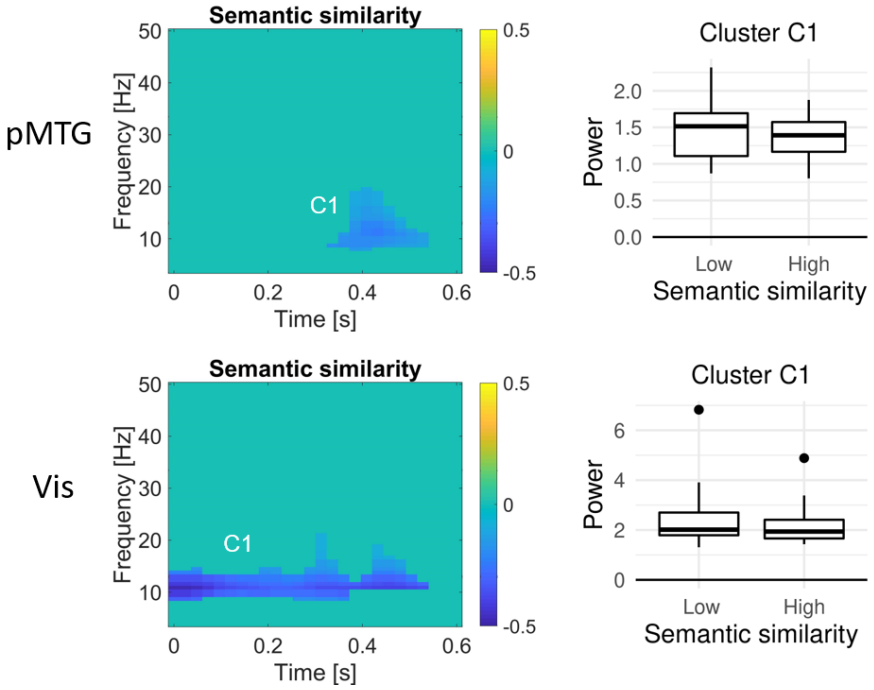


Figure 6. Oscillatory dynamics of the effect of semantic similarity (word2vec) during the processing of the second word in left pMTG, and bilateral visual cortex. Time-frequency plots show the difference between word pairs of high vs. low semantic similarity in significant clusters. Boxplots show the oscillatory power in each significant cluster for word pairs of high vs. low semantic similarity across participants. No significant effect of semantic similarity was found in the left IFG.

	Word 1 early	Word 1 late	Word 2 early	Word 2 late
IFG	γ: Unknown > Known θα: Known > Unknown		γ: Unknown > Known θα: Known > Unknown	
pMTG		θ: Known > Unknown		θ: Known > Unknown αβ: Less > More Similar
VIS			αβ: Unknown > Known	βγ: Unknown > Known
			αβ: Less > More Similar	

Figure 7. Summary of oscillatory dynamics. For each ROI, differences in oscillatory power between known and unknown goal trials in early (from 0 to 300 ms) and late time windows (from 300 to 600 ms) during the presentation of words 1 and 2 are presented. In case of significant main effects of knowledge, effects are indicated for both word 1 and word 2. For word 2, differences between less and more semantically similar word pairs are presented additionally. The frequency band of observed effects is indicated. Blue: Unknown > Known. Red: Known > Unknown. Black: Less > More Similar.

3.3 Spectral Granger Causality

We used spectral Granger Causality to investigate task knowledge effects and their interaction with word order on the effective connectivity between our three ROIs in early, intermediate and late time windows after word onset. In the early time window from 0 to 300 ms, connectivity from left IFG to left pMTG in the alpha band (Fig. 8a), as well as from left IFG to bilateral visual cortex in the beta band (Fig. 8b), was stronger in the unknown than in the known goal condition.

In the intermediate time window from 150 to 450 ms, a stronger connection in the known than in the unknown goal condition was found from IFG to visual cortex in the gamma band (Fig. 8c, 10b). Stronger connections in the unknown condition were found from pMTG to visual cortex in the beta band (Fig. 8d), and from visual cortex to IFG in the beta band (Fig. 8e, 10b). Furthermore, a significant interaction between task knowledge and word order was found for the connection from visual cortex to pMTG in the beta band (Fig. 9): For the first word, this connection was stronger in the known than in the unknown goal condition, while no significant difference between knowledge conditions was found for the second word. Furthermore, in the unknown condition, the strength of this connection increased from the first to the second word, while no significant difference between word 1 and 2 was found in the known condition.

In the final time window from 300 to 600 ms, the connections from the IFG to pMTG in the beta band (Fig. 8f), as well as from visual cortex to pMTG in the gamma band (Fig. 8g), were stronger in the known than in the unknown goal condition.

We did not observe significant effects of semantic similarity on Granger causality estimates in any of the investigated ROI pairs and time windows.

To summarize our key findings (Fig. 10), both IFG (in the early time window) and pMTG (in the intermediate time window) provided top-down feedback on visual cortex when

goals were absent. In contrast, with a known goal, only the IFG had a stronger top-down influence on visual cortex in the intermediate time window, which coincided with stronger feedforward signalling from visual cortex to pMTG. In the late time window, pMTG received stronger inputs from both IFG and visual cortex when goals were known, supporting the possibility of a greater convergence of information within the pMTG.

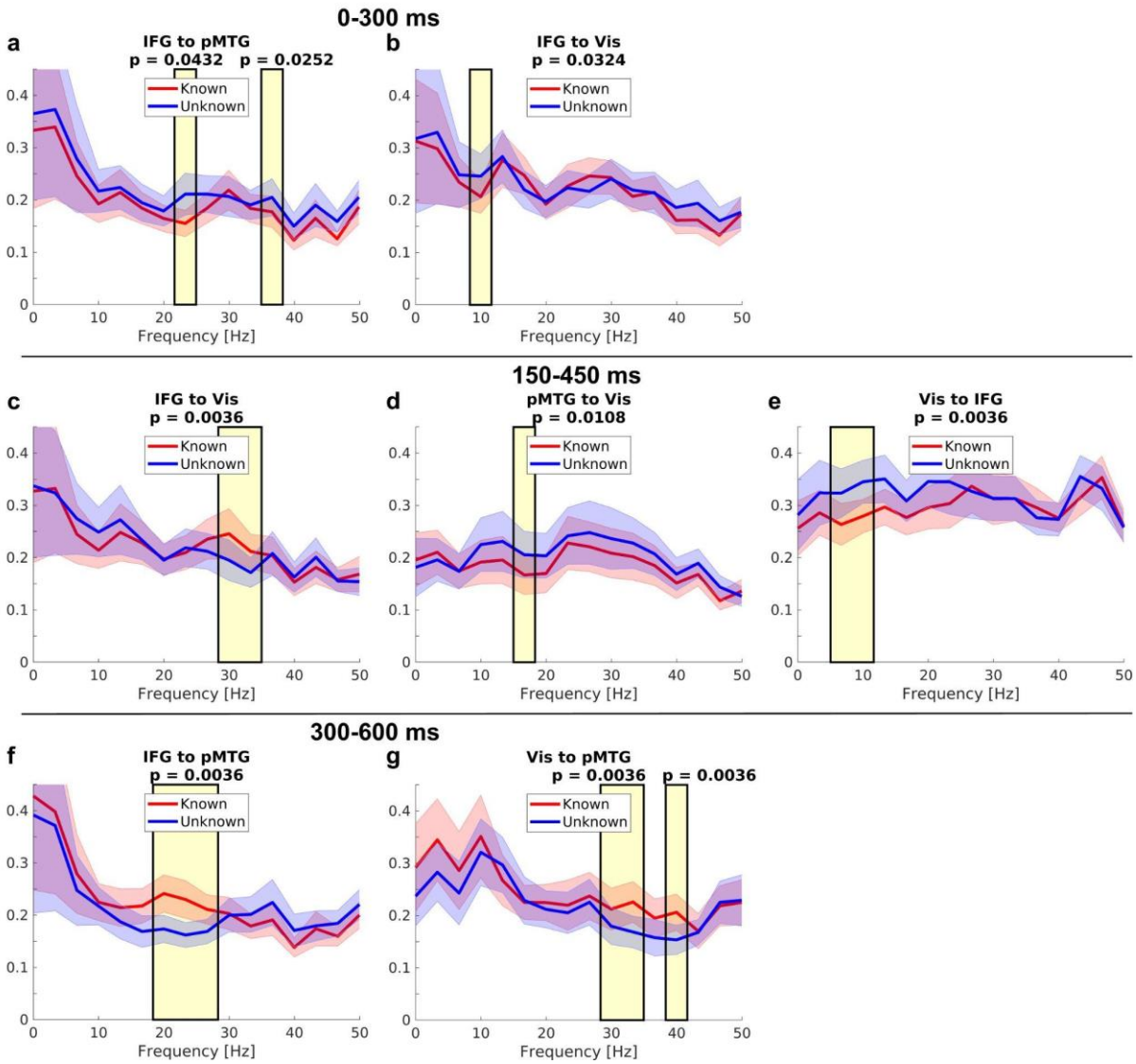


Figure 8. Main effects of task knowledge in spectral Granger causality estimates (averaged across word 1 and 2) in the time windows 0 to 300 ms, 150 to 450 ms, and 300 to 600 ms. Yellow shading indicates significant frequency ranges. Corresponding Bonferroni-corrected p-values are shown. Only significant effects of task knowledge on connectivity are plotted.

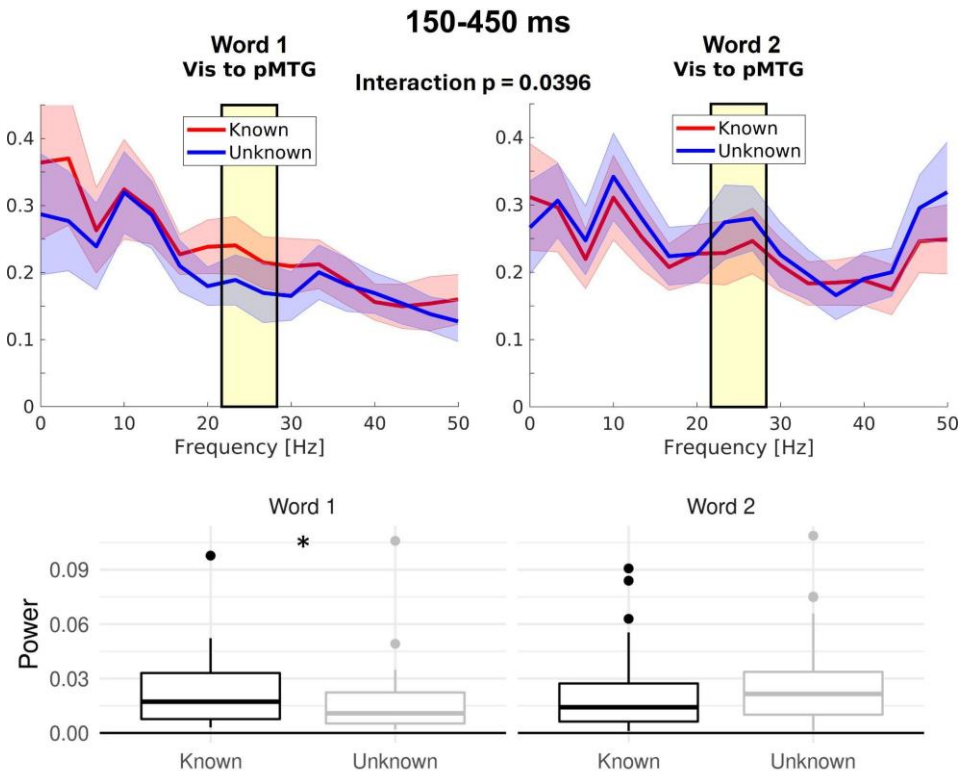


Figure 9. Interaction between task knowledge and word order in spectral Granger causality estimates in the time window 150 to 450 ms. Left, word 1; right, word 2. Yellow shading in line plots indicates the significant frequency range. The corresponding Bonferroni-corrected p-value is shown. Boxplots show the average power in the significant cluster across participants for each word and knowledge condition. Only significant connectivity interactions are plotted. The asterisk indicates a significant difference in a post-hoc test between the known and unknown goal conditions at the first word only.

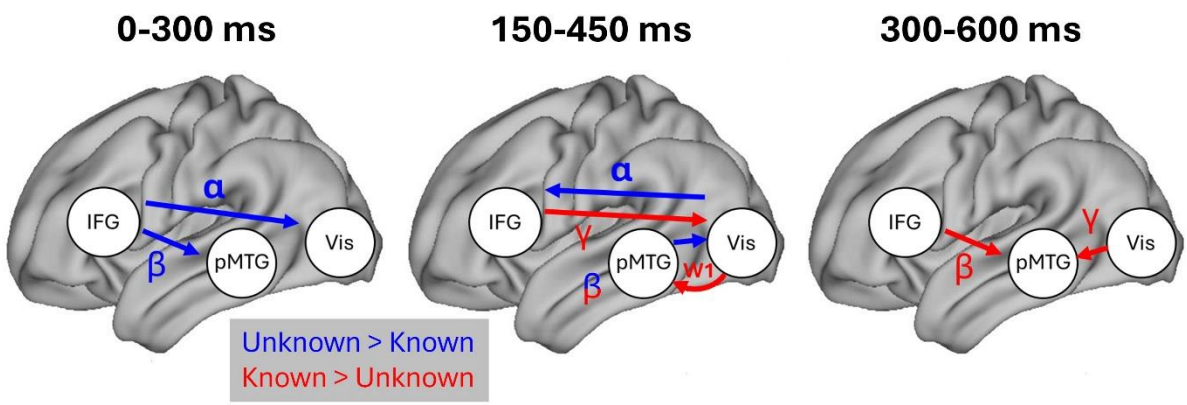


Figure 10. Effective connectivity based on spectral Granger causality estimates between left IFG, left pMTG and bilateral visual cortex in the time windows 0 to 300 ms, 150 to 450 ms, and 300 to 600 ms. Blue arrows show connections that are stronger in the unknown goal condition, while red arrows show connections that are stronger in the known goal condition. W1 indicates that the known > unknown difference was found at the first word, based on a significant interaction between task knowledge and word order and follow-up comparisons. The frequency range in which significant effects were found is also indicated. Only connections with a significant main effect of task knowledge, or a significant interaction between task knowledge and word order, are shown.

4 Discussion

Faced with the abundant semantic information associated with each concept, we rely on semantic control mechanisms within the left IFG and pMTG for the efficient retrieval of those features that are relevant to the current context and goals. The present investigation disentangles the roles of IFG and pMTG for controlled semantic cognition, indexed by their spectro-temporal profile and modulation of visual activity.

Both knowledge of the type of semantic relation and stronger semantic similarity between words enabled faster behavioural response times, in line with previous findings that contextual information facilitates semantic cognition (e.g., Mandera et al., 2017; Eisenhauer et al., 2019; 2022). However, both factors differentially affected MEG-measured oscillatory dynamics in the two semantic control regions (IFG and pMTG), as well as in visual cortex. Using MEG, we found that oscillatory theta/alpha power in the left IFG increased, while gamma power decreased when semantic goals were known in advance. Both patterns were found in similar time windows (peaking ~200 ms). In the left pMTG, higher theta power for known goals was only found in a later time window (peaking ~350 ms). In this later time window, the left pMTG was also sensitive to input-driven demands of semantic cognition: alpha/beta power for the second word was higher when it was less semantically similar to the first word, replicating previous findings (Teige et al., 2019). Our findings indicate that the semantic control network does not only engage more when semantic cognition is demanding (i.e., when semantic associations are weaker, e.g., Snyder et al., 2011; Krieger-Redwood et al., 2015; 2023; Teige et al., 2019) but also when semantic goals are explicitly known and facilitate semantic decisions (Grindrod et al, 2008; Zhang et al., 2021; cf. Wang et al., 2021). Specifically, our findings indicate that top-down goals are signalled sequentially in IFG and pMTG via low oscillations (theta/alpha), while the IFG also recruits higher gamma oscillations when goals are unknown. Participants may use task knowledge to narrow their expectations

about upcoming words, and the observed dissociation of oscillatory patterns fits to the proposed distinction from predictive coding theories of lower (alpha/beta) frequencies signalling top-down predictions and higher (gamma) frequencies signalling unexpected information (Arnal and Giraud, 2012, Michalareas et al., 2016). Potentially, distinct neural populations may underlie these opposing response patterns (Cope et al., 2023).

Semantic similarity and task knowledge effects were also found in visual cortex. Semantic similarity effects at the second word, i.e., higher alpha/beta power for less similar words, started at word onset and thus preceded similarity effects in pMTG, which may suggest that these effects propagated from the occipital to the temporal lobe in a purely bottom-up manner. In addition, no significant differences in effective connectivity were found between more and less similar word pairs. Thus, the present findings do not provide evidence for a modulation of visual semantic similarity effects by the semantic control network.

Task knowledge effects in visual cortex interacted with the bottom-up input, i.e., the order of the words: Only at the second word, alpha/beta power was reduced when semantic goals were known in advance, consistent with reduced fMRI activation observed previously for known goals at the second word (Zhang et al., 2021). This effect was found immediately after word onset, as well as towards the end of word presentation, suggesting that semantic goals facilitate visual processing both during the earliest stages as well as close in time to the semantic decision.

Importantly, task knowledge effects in visual cortex occurred only at the second word, while task knowledge effects in semantic control regions persisted during the processing of both words. This earlier occurrence of task knowledge effects in semantic control vs. visual regions is a first indication that activation in the semantic control network may modulate or ‘gate’ activation in visual cortex, as suggested by Zhang et al. (2021). To obtain more specific evidence, we used effective connectivity to directly investigate the direction and time-course

of connections between semantic control and visual regions. Corresponding to the findings of oscillatory power, top-down connectivity from the IFG to visual cortex could increase or decrease with task knowledge. In the goal unknown condition, top-down feedback from the IFG to visual cortex and pMTG (0-300 ms) preceded the bottom-up connection from visual cortex to IFG (150-450 ms). In the goal known condition, feedback from IFG to visual cortex occurred in the same time window (150-450 ms) as feedforward signalling from visual cortex to pMTG. This feedforward connection occurred at the first word only, indicating rapid feature retrieval when semantic goals are known. Thus, early top-down feedback from the semantic control network to visual regions (cf. Yvert et al., 2012; Schurz et al., 2014; Woodhead et al., 2014; Qin et al., 2021), that either precedes or coincides with bottom-up signalling from visual cortex, occurs both when semantic cognition is demanding but also when this difficulty can be resolved through explicit semantic goals. In the latter case, this process particularly relies on the IFG.

These findings provide strong evidence for the suggestion that the semantic control network shapes activation in visual cortex during semantic cognition (Zhang et al., 2021) and confirm the prediction from a computational model that successful semantic cognition depends on the feedback from control to unimodal input regions (Jackson et al., 2021). The IFG couples with visuo-temporal cortex during object (Xu et al., 2020) and face recognition (cf. Karimi-Rouzbahani et al., 2021) and reflects goals across various domains, including action perception (Wurm et al., 2014; Hrkać et al., 2015) and emotion regulation (Morawetz et al., 2016). Our findings thus generate predictions on how IFG modulates visuo-temporal activation in goal-dependent cognition across domains, which should be investigated in future research.

Finally, our research aimed at further elucidating the role of the left pMTG, which has been implicated in semantic control (Davey et al., 2016), but also in the storage of semantic representations (Schwartz et al., 2011, Teige et al., 2019) and lexical-semantic access (Dikker

et al., 2020). In the present study, pMTG exerted feedback on visual cortex only when semantic goals were unknown, suggesting that pMTG engages in visual control when processing demands are driven by absent contextual cues. When semantic goals were known, pMTG simultaneously received bottom-up input from visual cortex and top-down feedback from the left IFG, during presentation of both words in the latest investigated time window (300-600 ms). While previous studies found functional connections between IFG and pMTG at rest (Hallam et al., 2016; Wawrzyniak et al., 2017; Zhang et al., 2021) and during semantic cognition (Yue et al., 2013; Davey et al., 2016; Jackson et al., 2016), our findings reveal the directionality of this connection and its modulation by task knowledge. We did not find evidence that pMTG directly controls visual processing in goal-dependent semantic cognition. Rather, our findings suggest that pMTG integrates top-down semantic control from the IFG with bottom-up input from visual cortex, in line with the proposed necessity of such an integration region in computational modeling (Giallanza et al., 2024). The connectivity pattern of pMTG also corresponds with the suggestion that the IFG controls retrieval of lexical-semantic representations from pMTG (Lau et al., 2008). The temporal sequence of goal-dependent feedback from IFG to first visual cortex and then pMTG might reflect a shift from initial visual to later lexical-semantic feature retrieval.

A limitation of the present study is the use of a simple semantic context with a relatively small variance in semantic similarity, and it remains to be investigated if the same mechanisms generalize to more naturalistic contexts (Deniz et al., 2023). However, the advantages of a simple context are the explicit experimental control of semantic goals and reduced variability from the linguistic input. Furthermore, the present findings cannot dissociate if reduced activation in visual cortex reflects facilitated recognition of letters/orthography (Eisenhauer et al., 2019), and/or facilitated retrieval of visual-semantic features of the corresponding object (Chiou et al., 2018; Zhang et al., 2021). Moreover, while previous studies varying linguistic

context mainly found desynchronized alpha/beta oscillations (Prystauka and Lewis, 2019), we observed synchronization across all frequency bands. Possibly, the temporal onset predictability of the presented words based on the preceding cue may have driven synchronized responses. While the interpretations of connections at particular frequencies remain unclear, the majority of our findings are consistent with the assumption that shorter connections utilize relatively higher frequencies (von Stein and Sarnthein, 2000).

To conclude, we found that core regions of the semantic control network engage differently during semantic cognition: While both regions increase their oscillatory power based on the presence of semantic goals, this occurs earlier in IFG than in pMTG. The two regions also strongly diverged in their interactions with visual cortex: IFG modulated visual activation via top-down feedback, which coincided with increased early feedforward signalling from visual cortex, suggesting that known semantic goals enable the rapid controlled retrieval of task-relevant features. In contrast, pMTG received inputs from both IFG and visual cortex in a later time window. This indicates that IFG *controls* goal-dependent retrieval, while pMTG *integrates* top-down semantic control with bottom-up input.

Tables

Table 1. Stimulus Characteristics.

		Minimum	1st Quartile	Median	Mean	3rd Quartile	Maximum
Word 1 Length	**Taxonomic**	3.00	4.00	5.00	5.55	7.00	10.00
	Thematic	3.00	4.00	6.00	5.77	7.00	9.00
	Unrelated	3.00	5.00	5.50	5.78	7.00	10.00
Word 2 Length	**Taxonomic**	3.00	4.00	5.00	5.61	7.00	10.00
	Thematic	3.00	4.00	5.00	5.65	7.00	10.00
	Unrelated	2.00	4.00	5.00	5.75	7.00	10.00
Word 1 Frequency	**Taxonomic**	0.00	0.61	0.92	0.98	1.33	2.44
	Thematic	0.00	0.65	1.02	1.03	1.36	2.75
	Unrelated	0.14	0.61	0.96	0.96	1.27	2.13
Word 2 Frequency	**Taxonomic**	0.19	0.69	0.93	1.03	1.27	2.59
	Thematic	0.00	0.80	1.09	1.10	1.42	2.10
	Unrelated	0.21	0.56	0.92	1.02	1.37	2.44
Word 1 Imageability	**Taxonomic**	276.00	555.00	586.00	573.10	602.00	652.00
	Thematic	376.00	541.00	580.00	564.50	607.50	655.00
	Unrelated	390.00	553.50	587.00	575.70	614.80	640.00
Word 2 Imageability	**Taxonomic**	232.00	560.50	580.50	575.80	609.00	655.00
	Thematic	232.00	553.50	581.20	565.90	605.00	642.00
	Unrelated	398.00	545.80	595.00	578.30	612.00	652.00
Semantic Similarity (word2vec)	**Taxonomic**	0.10	0.25	0.32	0.32	0.40	0.62
	Thematic	0.04	0.19	0.27	0.27	0.34	0.60
	Unrelated	-0.04	0.03	0.08	0.08	0.13	0.26

Table 2. Results of the simple linear mixed model of behavioural response times.			
	FE	SE	*t*
Intercept	**2.995**	**0.024**	**126.65**
Task Knowledge	**0.023**	**0.006**	**4.05**
Semantic Relation	0.003	0.007	0.43
Semantic Similarity (word2vec)	**-0.020**	**0.004**	**-5.54**
Trial Order	**-0.024**	**0.002**	**-11.20**
Instruction	-0.015	0.023	-0.65
Task Knowledge x Semantic Relation	-0.010	0.008	-1.22
Task Knowledge x Semantic Similarity (word2vec)	0.003	0.004	0.84
Bold numerals indicate significant effects, i.e., $\|t\| > 2$. FE = fixed effect estimates; SE = standard error.			

Table 3. Results of the complex linear mixed model of behavioural response times.			
	FE	SE	t
Intercept	**2.991**	**0.024**	**122.37**
Task Knowledge	**0.021**	**0.007**	**3.11**
Semantic Relation	-0.002	0.008	-0.23
Semantic Similarity (word2vec)	**-0.021**	**0.004**	**-4.82**
Trial Order	**-0.022**	**0.003**	**-8.87**
Instruction	-0.015	0.024	-0.61
Word 1 Length	**-0.009**	**0.004**	**-2.31**
Word 2 Length	-0.007	0.004	-1.59
Word 1 Frequency	0.003	0.004	0.76
Word 2 Frequency	-0.005	0.004	-1.29
Word 1 Imageability	0.003	0.003	0.91
Word 2 Imageability	**-0.009**	**0.004**	**-2.32**
Task Knowledge x Semantic Relation	-0.005	0.010	-0.53
Task Knowledge x Semantic Similarity (word2vec)	0.001	0.005	0.20

Bold numerals indicate significant effects, i.e., $\|t\| > 2$. FE = fixed effect estimates; SE = standard error.

Table 4. Results of the simple generalized linear mixed model of behavioural accuracies.

	FE	SE	*z*	*p*
Intercept	**1.758**	**0.174**	**10.09**	**< 2e-16**
Task Knowledge	0.041	0.113	0.36	0.7162
Semantic Relation	0.016	0.155	0.10	0.9178
Semantic Similarity (word2vec)	**0.286**	**0.080**	**3.60**	**0.0003**
Trial Order	0.037	0.040	0.92	0.3580
Instruction	0.076	0.138	0.55	0.5832
Task Knowledge x Semantic Relation	**-0.342**	**0.159**	**-2.15**	**0.0312**
Task Knowledge x Semantic Similarity (word2vec)	-0.077	0.081	-0.96	0.3392

Bold numerals indicate significant effects, i.e., $p < 0.05$. FE = fixed effect estimates; SE = standard error.

Table 5. Results of the complex generalized linear mixed model of behavioural accuracies.

	FE	SE	*z*	*p*
Intercept	1.803	0.184	9.82	< 2e-16
Task Knowledge	-0.043	0.134	-0.32	0.748
Semantic Relation	0.006	0.180	0.04	0.971
Semantic Similarity (word2vec)	**0.377**	**0.097**	**3.89**	**0.0001**
Trial Order	-0.029	0.049	-0.60	0.552
Instruction	0.101	0.139	0.73	0.467
Word 1 Length	-0.015	0.084	-0.17	0.863
Word 2 Length	0.137	0.096	1.43	0.154
Word 1 Frequency	0.000	0.088	0.00	0.998
Word 2 Frequency	0.079	0.086	0.92	0.359
Word 1 Imageability	0.140	0.073	1.91	0.056

Word 2 Imageability	**0.222**	**0.084**	**2.64**	**0.008**
Task Knowledge x Semantic Relation	-0.198	0.197	-1.00	0.315
Task Knowledge x Semantic Similarity (word2vec)	-0.069	0.101	-0.68	0.495
Bold numerals indicate significant effects, i.e., $p < 0.05$. FE = fixed effect estimates; SE = standard error.				

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