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Citation for published version:

Thye, M, Geller, J, Szaflarski, JP & Mirman, D 2021, 'Intracranial EEG evidence of functional specialization for taxonomic and thematic relations', *Cortex*, vol. 140, pp. 40-50.
<https://doi.org/10.1016/j.cortex.2021.03.018>

Digital Object Identifier (DOI):

[10.1016/j.cortex.2021.03.018](https://doi.org/10.1016/j.cortex.2021.03.018)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Peer reviewed version

Published In:

Cortex

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Intracranial EEG evidence of functional specialization for taxonomic and thematic relations

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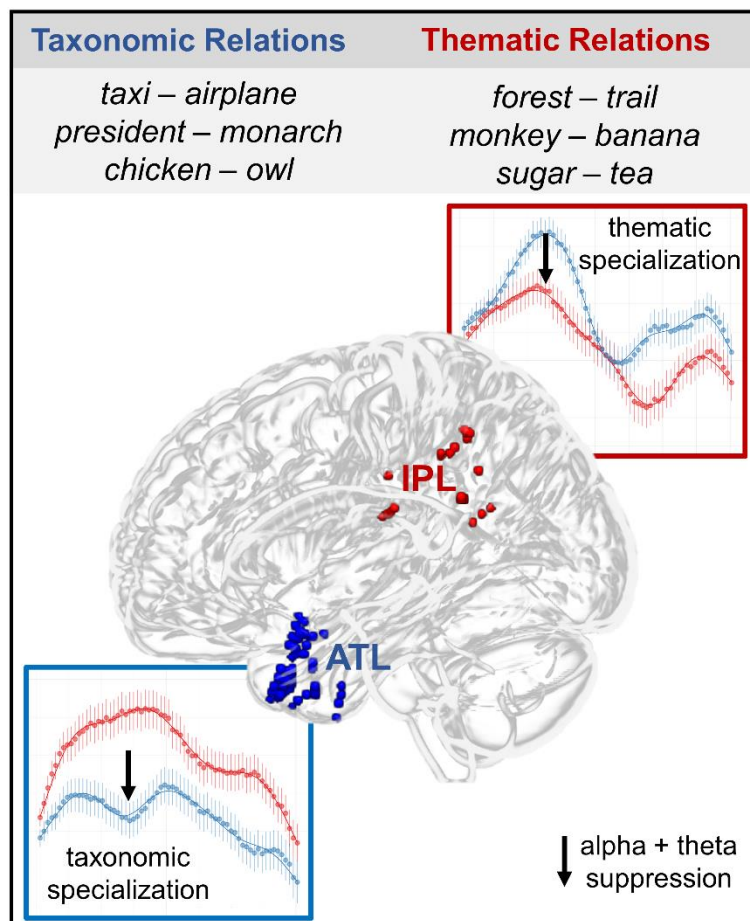
Highlights

- Neural organization of the semantic system may be specialized by type of relation
- Intracranial EEG was used to examine the semantic brain network dynamics
- The anterior temporal lobe is specialized for taxonomic or feature-based relations
- The inferior parietal lobule is specialized for thematic or event-based relations

Abstract

The dual-hub account posits that the neural organization of semantic knowledge is segregated by the type of semantic relation with anterior temporal lobe (ATL) specializing for taxonomic relations and inferior parietal lobule (IPL) for thematic relations. This study critically examined this account by recording intracranial EEG from an array of depth electrodes within ATL, IPL, and two regions within the semantic control network, inferior frontal gyrus (IFG) and posterior middle temporal gyrus (pMTG), while 17 participants with refractory epilepsy completed a semantic relatedness judgment task. We observed a significant difference between relation types in ATL and IPL approximately 600-800ms after trial presentation, and no significant differences in IFG or pMTG. Within this time window, alpha and theta suppression indexing cognitive effort and memory retrieval was observed in ATL for taxonomic trials and in IPL for thematic trials. These results suggest taxonomic specialization in ATL and thematic specialization in IPL, consistent with the dual-hub account of semantic cognition.

Keywords: semantic cognition, intracranial EEG, taxonomic, thematic



1. Introduction

Semantic knowledge is an integral aspect of human cognition. It provides an interpretive framework through which humans interact with their environment and attribute meaning to the objects and events they encounter (Kumar, 2020; McRae & Jones, 2013). Models of semantic memory predominately account for taxonomic relations, focusing on feature overlap to assign concrete concepts into categories within a hierarchical structure (Binney, Embleton, Jefferies, Parker, & Lambon Ralph, 2010; Lambon Ralph, Jefferies, Patterson, & Rogers, 2017; Patterson, Nestor, & Rogers, 2007). In addition to these taxonomic relations, semantic knowledge also includes thematic relations based on shared context or co-occurrence of events (Binder, Desai, Graves, & Conant, 2009; Goldwater, Markman, & Stilwell, 2011; Mirman & Graziano, 2012; Mirman, Landrigan, & Britt, 2017; Schwartz et al., 2011). The process of acquiring thematic knowledge is distinct from that of taxonomic knowledge (Estes, Golonka, & Jones, 2011), and there is a processing time cost to switching between taxonomic and thematic relations (Landrigan & Mirman, 2018). This suggests that these are distinct semantic systems. A recent systematic review found that there are consistent individual differences in strength of taxonomic versus thematic semantic knowledge, that taxonomic and thematic relations make independent contributions to relatedness, and that they have different time courses of activation (Mirman et al., 2017). The systematic review also suggested differences in the neural basis of taxonomic and thematic semantic cognition, but these results were mixed.

There are two opposing accounts of semantic cognition that make different predictions about how taxonomic and thematic knowledge are represented and retrieved in the semantic brain network. The first account, the hub-and-spoke model, posits that the anterior temporal lobes (ATLs), which have been consistently identified as central to semantic cognition (Binney et al., 2010; Lambon Ralph et al., 2017; Patterson et al., 2007; Wong & Gallate, 2012), serve as transmodal hubs integrating information from surrounding sensorimotor spokes to arrive at semantic representations (Lambon Ralph, Sage, Jones, & Mayberry, 2010; Rogers et al., 2004). Within the hub-and-spoke model, no neural dissociation would be seen in processing taxonomic and thematic relations. A number of studies have reported such dissociations, however (de Zubicaray, Hansen, & McMahon, 2013; Geng & Schnur, 2016; Kalénine & Buxbaum, 2016; Kalénine et al., 2009; Sass, Sachs, Krach, & Kircher, 2009; Schwartz et al., 2011; Tsagkaridis, Watson, Jax, & Buxbaum, 2014; Wu, Waller, & Chatterjee, 2007; Xu et al., 2018). The second theoretical account, the dual-hub model, suggests that the central role of ATL in models of semantic cognition may be driven, in part, by the over-representation of studies examining taxonomic relations and the difficulty of constructing stimuli and tasks that effectively distinguish taxonomic and thematic relations without introducing differential cognitive demands. In addition, meta-analyses of semantic cognition have identified a possible second semantic hub which supports retrieval of thematic semantic knowledge in the inferior parietal lobule (IPL), comprised of the supramarginal and angular gyri (Binder & Desai, 2011; Binder et al., 2009; Jefferies, Thompson, Cornelissen, & Smallwood, 2019). The “dual-hub” view suggests that this IPL hub is specialized for thematic relations whereas the ATL hub is specialized for taxonomic relations (Mirman et al., 2017; Xu et al., 2018).

A related extension of the hub-and-spoke-model, the controlled semantic cognition (CSC) framework, additionally highlights the role of a semantic control system, comprised of the inferior frontal gyrus (IFG) and posterior middle temporal gyrus (pMTG) that works alongside the semantic system in directing and constraining the retrieval of relevant semantic knowledge (Jefferies et al., 2019; Lambon Ralph et al., 2017; Thompson et al., 2017; Whitney, Kirk, O’Sullivan, Lambon Ralph, & Jefferies, 2011; Zhang et al., 2020). This semantic control system is especially relevant for retrieving weak semantic relations and selecting task-relevant information. The CSC framework makes two

important observations regarding the taxonomic-thematic distinction. First, taxonomically related objects share properties that are inherent to the objects themselves and feature comparison can be done quickly and efficiently. Thematic relations (especially weak relations), however, are not inherent to the objects themselves, so the relevant contextual information must be retrieved, often (though not always) requiring additional semantic control (Thompson et al., 2018; Whitney et al., 2011; Zhang et al., 2020). Second, there is a functional dissociation between the pMTG, which is part of the semantic control system, and the IPL, which is engaged during “automatic” semantic retrieval (Jefferies et al., 2019). The proximity of these regions may have led prior studies to confuse engagement of the pMTG during control-demanding thematic tasks with automatic semantic retrieval supported by IPL. Within the CSC framework, the angular gyrus works alongside ATL in retrieving strong semantic relations and neither region is specialized for processing specific semantic relations, while IFG and pMTG form a semantic control system that is engaged for weak semantic relations or otherwise retrieval-demanding semantic tasks (Jefferies et al., 2019; Thompson et al., 2017). Support for this position was seen in a MEG study which found that ATL showed a greater response for taxonomic relations whereas thematic relations elicited a stronger response in pMTG. In addition, ATL responded more on strongly related trials, whereas pMTG responded more on weakly related trials, highlighting the role of this region in semantic control (Teige et al., 2019).

The primary aim of the present study was to directly compare the single-hub and dual-hub accounts of semantic cognition by assessing neural responses to taxonomic and thematic relations using a method with high spatial and temporal resolution. Previous studies of semantic cognition have been restricted to neuroimaging methods with limited spatial (centimetre) and temporal (second) resolution, which are not capable of fully exploring the dynamics of the semantic system. Stereoelectroencephalography (sEEG), records directly from an array of depth electrodes implanted throughout the brain and, therefore, captures the spatio-temporal transitions within networks on a much finer neuroanatomical (millimeter) and temporal (millisecond) scale providing an ideal avenue to study semantic processing. A secondary aim was to evaluate whether taxonomic and thematic relations differentially recruit semantic control regions when task demands are matched (i.e., using highly related pairs). This provides an opportunity to directly test the predictions of the CSC framework and leverage the spatial resolution provided by intracranial EEG to dissociate the contributions of pMTG and IPL within the semantic system. The key neural measures in the present study were spectral power in the theta (4-7 Hz), alpha (8-12 Hz), and high gamma (70-150 Hz) bands, which have been used in previous intracranial EEG studies as indices for memory recall (Herweg, Solomon, & Kahana, 2020), active engagement (Klimesch, 2012), and higher-order cognition (Jia & Kohn, 2011), respectively. Specifically, decreases in the theta and alpha power (i.e., alpha suppression) are associated with successful memory retrieval and increased attention, effort, or task engagement (Drijvers, Özyürek, & Jensen, 2018; Herweg et al., 2020). Analogous decreases in low frequency power during memory retrieval and attention have been reported across a broad network of left hemisphere language regions (Solomon et al., 2017; Weidemann et al., 2019). Although low frequency power was of primary interest, high gamma band power strongly correlates with BOLD activation and thus provides complementary information albeit at a much finer spatiotemporal resolution (Engell, Huettel, & McCarthy, 2012; Lachaux et al., 2007).

In line with the dual-hub account, it was hypothesized that decreased theta and alpha power would be observed in ATL on taxonomic trials (relative to thematic trials) and in IPL on thematic trials (relative to taxonomic trials). The converse pattern should be observed in the high gamma band: increased power in ATL on taxonomic trials (relative to thematic trials) and in IPL on thematic trials (relative to taxonomic trials). Regarding the secondary aim of investigating the claims of the controlled semantic cognition framework, thematic semantic retrieval was not expected to pose

additional control demands especially when stimuli were designed to have minimal semantic control demands, so no differences in processing taxonomic and thematic trials were expected within the semantic control regions (IFG and pMTG). Neither the single-hub nor dual-hub account make claims about the time course of processing taxonomic and thematic relations, so this is left as an exploratory element of this study. The temporal resolution of intracranial EEG provides a unique opportunity to understand how activation within the semantic system unfolds on a millisecond timescale which, when combined with the spatial specificity of the data, can augment current knowledge and yield new predictions about the neural basis of semantic cognition.

2. Methods

2.1 Participants

Thirty-one patients with refractory epilepsy took part in this study after written informed consent was obtained. All participants were undergoing in-patient phase II video and EEG monitoring to localize seizure onset in preparation for possible surgical resection; all were tested at least 24 hours after implantation of electrodes and were sufficiently recovered from the anesthesia as documented by normal (or at baseline) neurological examination before obtaining consent and performing study procedures. All determinations of the return to normal (or baseline) neurological examination were performed by a neurologist or neurosurgeon not affiliated with the study. SEEG electrode localization was determined by evaluation needs (standard of care) and additional electrodes were not added for the purpose of this study. Participants were excluded from analysis if they had low accuracy (<60%) in either task condition (n=2), both Full Scale and Verbal IQ in the mildly impaired range (<70) (n=2), seizure activity during the task (n=1), errors in data recording (n=3), or lack of electrodes in the regions of interest (n=6). Exclusion criteria were established prior to data analysis. The final sample for analysis consisted of 17 participants. The demographic and neuropsychological information is provided in Table 1. The participant-level electrode coverage within each region of interest is provided in Supplemental Table 1. The study was carried out in accordance with protocols approved by the Institutional Review Board at the University of Alabama at Birmingham. All participants signed an informed consent.

Table 1

Participant Information

	N	Mean (SD)	Range
Age (years)	17	35.75 (8.79)	24-49
Full Scale IQ	16	87.38 (19.09)	61-129
Verbal IQ	17	94.82 (19.27)	63-130
Semantic Fluency	14	17.43 (5.12)	9-24
Accuracy (%)			
<i>Taxonomic Trials</i>	17	83.82 (11.49)	68.75-100
<i>Thematic Trials</i>	17	86.40 (10.88)	62.50-100
Reaction Time (s)			
<i>Taxonomic Trials</i>	17	4.11 (1.87)	1.12-8.47
<i>Thematic Trials</i>	17	3.99 (2.29)	1.21-9.52
Sex (M:F)	6:11		
Race (B:W)	6:11		
	N	No. Channels	Coverage Mean (Range)
ATL	8	56	7 (4-10)

IPL	6	25	4 (1-8)
IFG	16	116	7 (2-12)
pMTG	14	62	4 (1-11)

Note. Semantic fluency scores were derived by asking participants to list as many animals as they could within one minute. N, number of participants; SD, standard deviation of the mean; s, seconds; No., number; M, Male; F, Female; B, Black; W, White; ATL, anterior temporal lobe; IPL, inferior parietal lobule; IFG, inferior frontal gyrus; pMTG, posterior middle temporal gyrus; Coverage Mean (Range), mean number of electrode channels and the range of coverage for participants with electrodes within each region (indicated by N).

2.2 Materials

Participants completed a semantic relatedness judgment task that has been used in a previous study with neurologically typical participants (Geller, Landrigan, & Mirman, 2019). Critical word pairs were derived from publicly available word norms of taxonomic and thematic relations (Landrigan & Mirman, 2016) and differed in the type of semantic relationship (taxonomic or thematic) and the strength of the semantic relationship (strongly related or weakly related). The stimuli and word properties are available on the project OSF page (<https://osf.io/xtfah/>). Only the strongly related trials were analysed in the current study (Supplemental Table 2)^a. These strongly related stimuli were previously found to be matched in terms of control demands based on response times, accuracy, and a psychophysiological measure of cognitive effort (i.e., task-evoked pupillary response (TEPR); Geller et al., 2019). Filler trials of unrelated word pairs comprised 50% of the total number of trials. Conditions were matched on word length (in letters, syllables, and phonemes), word frequency (Brysbaert & New, 2009), imageability, and orthographic neighbourhood size.

2.3 Procedure

Participants completed an approximately one-hour testing session consisting of four language tasks during continuous sEEG monitoring. Intracranial video-EEG from an array of multi-contact depth electrodes (8-16 contacts, 2 mm contact length, 0.8 mm contact diameter, 1.5 mm inter-contact distance) were recorded using Natus Xltek with sampling at 2 kHz to allow for better processing of the signal.

All tasks were administered in each participant's hospital room via a laptop positioned within arm's reach of the participant on an adjustable table. Task instructions were presented on screen and explained verbally, and participants completed several practice trials prior to beginning each task. During the semantic relatedness task, two words appeared on the screen, and participants were asked to judge whether the words were related or unrelated. Responses were indicated via the laptop keyboard using the "Z" key for related and the "M" key for unrelated. A total of 128 trials (64 critical trials, 16 in each condition) were presented in random order with an inter-trial interval of 2000ms during which participants saw a fixation cross. Trials were presented within 8 discrete blocks, and participants were given a break after each block. Trial onset signals from the experiment

^a Accuracy on weakly related trials was relatively poor across participants ($M = 73.5\%$) and below the 60% threshold for 6 of the 17 participants, which drastically reduces the sample size and makes the data unreliable both statistically (error trials were excluded, so the number of analysed trials would be low) and theoretically (with accuracy close to the 50% chance level for several participants, even the correct responses could be guesses, so it cannot be assumed that the correct semantic relations were retrieved on those trials either).

software were converted into TTL pulses by a custom-built Arduino device to mark trial onsets in the EEG data. All tasks were programmed in E-Prime 2.0 software (Psychology Software Tools, 2016).

2.4 Data Preprocessing

Participant pre-operative MRI scans were processed through FreeSurfer (Dale, Fischl, & Sereno, 1999) to generate a cortical surface mesh and co-registered with the post-implantation CT scan. Electrodes were manually localized in native space by identifying the centre of the visible artefact on the CT scan using the iElectrodes program (Blenkmann et al., 2017). Electrode coordinates were normalized to template space using the MATLAB-based FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011) and referenced to standard atlases using code adapted from Stolk et al. (Stolk et al., 2018). Electrode locations were visualized by generating a 3mm sphere around each normalized coordinate using AFNI (Cox, 1996).

Signal data were processed in MATLAB 2019a (MATLAB, 2019) using the signal processing and FieldTrip toolboxes. A detailed overview of the pipeline and the code used to run all analyses are available on OSF (<https://osf.io/xtfah/>). Data were segmented into 2500ms windows capturing the trial and baseline period (500ms). Trials were demeaned and line noise around 60Hz (and its 2nd and 3rd order harmonics) was attenuated with a notch filter. Data were visually inspected, and channels with excessive spiking across trials were removed (n=25). An automated artefact rejection algorithm was run on the z-transformed data (threshold = 7), and trials which contained an artefact were excluded from analysis. Data were downsampled to 500Hz and each channel was re-referenced to the median value of the other channels on the electrode shaft. The resulting data were bandpass filtered using a 6th order Butterworth filter to separately extract the theta band (4-7Hz), the alpha band (8-12Hz), and high gamma band (70-150Hz). The Hilbert transform was applied to compute the analytic signal within each of the extracted frequency bands, and the data were smoothed using overlapping sliding windows of 250ms every 30ms and baseline corrected using the percent change from the 300ms prior to the trial onset.

Data were recorded from a total of 1298 electrodes contacts for the 17 participants included in the analysis, of which 1039 were excluded from analyses due to the presence of excessive artefacts or placement outside of the regions of interest (ROIs). The ROIs were derived using the cortical parcellation of several atlases due to the lack of a clearly defined ATL or IPL region in any single atlas, although there was significant overlap in the region definitions across atlases. The left ATL region was comprised of the middle and superior temporal pole regions within the AAL atlas (Tzourio-Mazoyer et al., 2002), the temporal pole region with the Harvard-Oxford atlas, and the temporal pole region within the Destrieux atlas (defined in participant native space) (Destrieux, Fischl, Dale, & Halgren, 2010). The left IPL region was comprised of the supramarginal and angular gyri regions within the AAL atlas and the supramarginal region within the Desikan-Killiany atlas (defined in participant native space) (Desikan et al., 2006). The left IFG region was comprised of the orbital, triangular, and opercular parts of the inferior frontal gyrus in the AAL atlas, and the IFG region within the Brainnetome (Fan et al., 2016) and AFNI Talairach-Tournoux (Lancaster et al., 1997) atlases. The left PMTG region was defined as the posterior division and the temporo-occipital part of the middle temporal gyrus within the Harvard-Oxford atlas. See Figure 1 for electrode coverage across participants within the regions of interest and the location of the electrodes within each ROI.

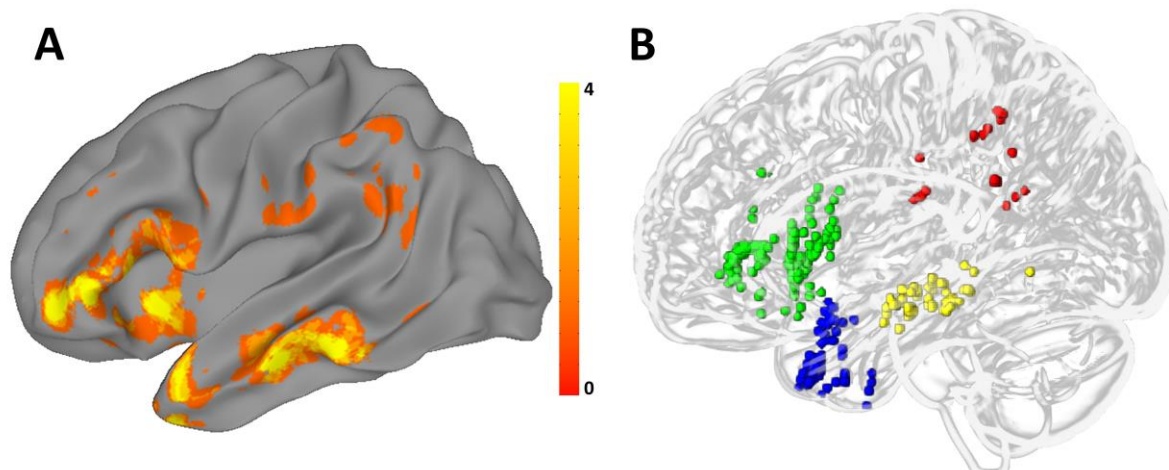


Figure 1. (A) Spatial coverage map illustrating the number of participants with electrodes in the same brain areas. Electrodes which fall outside of the regions of interest are not shown. (B) Electrodes within each region of interest (ATL – blue; IPL – red; IFG – green; pMTG – yellow).

2.5 Statistical Analysis

Filler, weakly related, inaccurate (14.9%), and slow response (RT > 10s; 6.8%) trials were removed prior to analysis. The statistical analyses were conducted using a 2s window starting at stimulus onset. To capture changes in the time course of activation, the data were analysed using generalized additive mixed models (GAMMs; Winter & Wieling, 2016; Wood, 2017). GAMMs have several advantages compared to more widely adopted point-by-point methods: (1) GAMMs are more conservative and do not require a multiple comparisons correction. (2) Complex nonlinear relationships can be modelled flexibly while accounting for variation that may arise across participants, trials, and electrodes. This is especially relevant for modelling the fluctuations in the neural signal over the course of the extracted time window. (3) An autoregressive model component can be included to limit the autocorrelation of errors which poses a significant concern in direct analyses of time series data (Baayen, Rij, Cat, & Wood, 2018). (4) Of particular relevance for the data analysed here, the GAMM approach of fitting smooth splines is a better representation of the underlying data generating process. In contrast, point-by-point comparisons treat each point as an independent observation. This modelling approach has been applied to pupillometry (van Rij, Hendriks, van Rijn, Baayen, & Wood, 2019), eye-tracking, and event-related potentials (Porretta, Tremblay, & Bolger, 2017), highlighting the applicability of GAMMs to a variety of non-linear time series data.

A generalized additive mixed model was run for each ROI predicting the log-transformed signal (Smulders, ten Oever, Donkers, Quaedflieg, & van de Ven, 2018) within each frequency band with fixed effects of trial type (taxonomic vs. thematic), a general smooth effect of time to model the nonlinear change in the signal across the trial duration, and a smooth over time effect for each trial type (i.e., time course differences between taxonomic and thematic conditions). The random effects structure consisted of a by-participant-electrode factor smooth over time (time course differences between individual participant electrodes) and a random intercept of subject-trial. Individual differences across electrodes within subjects and trials within subjects are thus captured within the

model specification.^b Due to high autocorrelation of the residuals within the time series ($\rho = 0.92-0.97$), the first-order autoregressive model was accounted for in the model estimation. Smoothing was estimated via restricted maximum likelihood (REML). Model predictions were used to isolate the windows of time where the signal differed by trial type. This was done by calculating the difference curve between the fitted smooth condition terms from the model predictions using simulation-derived simultaneous 95% confidence intervals. The statistical analyses were run in R using the *mgcv* (Wood, 2004) and *itsadug* (van Rij, Wieling, Baayen, & van Rijn, 2020) packages. The data and code used to run the analysis and additional details regarding the diagnostic plots and model specification are available on OSF (<https://osf.io/xtfah/>).

3. Results

There were no significant differences in accuracy ($t(16) = 1.05, p = 0.31$) or reaction time ($t(16) = -0.27, p = 0.79$) between the taxonomic and thematic trials, consistent with previously reported behavioural results from a sample of neurotypical adults (Geller et al., 2019) and further indicating that the control demands were comparable for each condition.

The model estimates for the fixed and random effects are presented in Supplemental Table 3. These parameter estimates do not directly answer the research questions, but the model predictions were used to identify time intervals with statistically significant condition differences. Figure 2 shows the signal time course for each frequency band in each ROI for taxonomic and thematic conditions, with time intervals with statistically significant differences between conditions shown by dashed lines.^c

3.1 Theta

Within the ATL, theta band power was significantly lower on taxonomic trials compared to thematic trials from 597 to 886ms after the trial onset. The opposite pattern was observed in the IPL with lower theta band power on thematic compared to taxonomic trials from 717 to 806ms and again from 1264 to 1622ms after trial onset. There were no significant windows of time where the signal differed by condition in either IFG or pMTG.

3.2 Alpha

The pattern of results in the alpha band was similar to the theta band. Within the ATL, alpha band power was significantly lower on taxonomic trials compared to thematic trials from 547 to 726ms after trial onset. In IPL, alpha band power was lower on thematic trials compared to taxonomic trials from 577 to 766ms. There were no significant differences between the conditions across the time course in either IFG or pMTG.

3.3 High Gamma

Unlike the theta and alpha bands, the course of high gamma band power was highly variable, with only a small window of significant difference between taxonomic and thematic trials: greater high

^b The models were also run with reaction time included as a fixed effect, and the results were the same. Reaction time was not a significant predictor ($p > .10$) in all but one model (alpha band analysis within IFG: $p = 0.02$). Model comparisons indicated that the models without the fixed effect of reaction time were preferred. Therefore, the statistically preferred models without the reaction time effect are reported here. Additional information on the reaction time analyses are available on the project OSF page.

^c The results from a cluster-based permutation analysis approach largely converged with the results reported here with the exception of additional time windows of significant condition difference due to the less conservative nature of this analysis. Additional information regarding these analyses are available on the project OSF page.

gamma band power in ATL on taxonomic trials compared to thematic trials from 1115 to 1194ms^d. There were no significant differences between the conditions across the time course in the IPL, IFG, or pMTG.

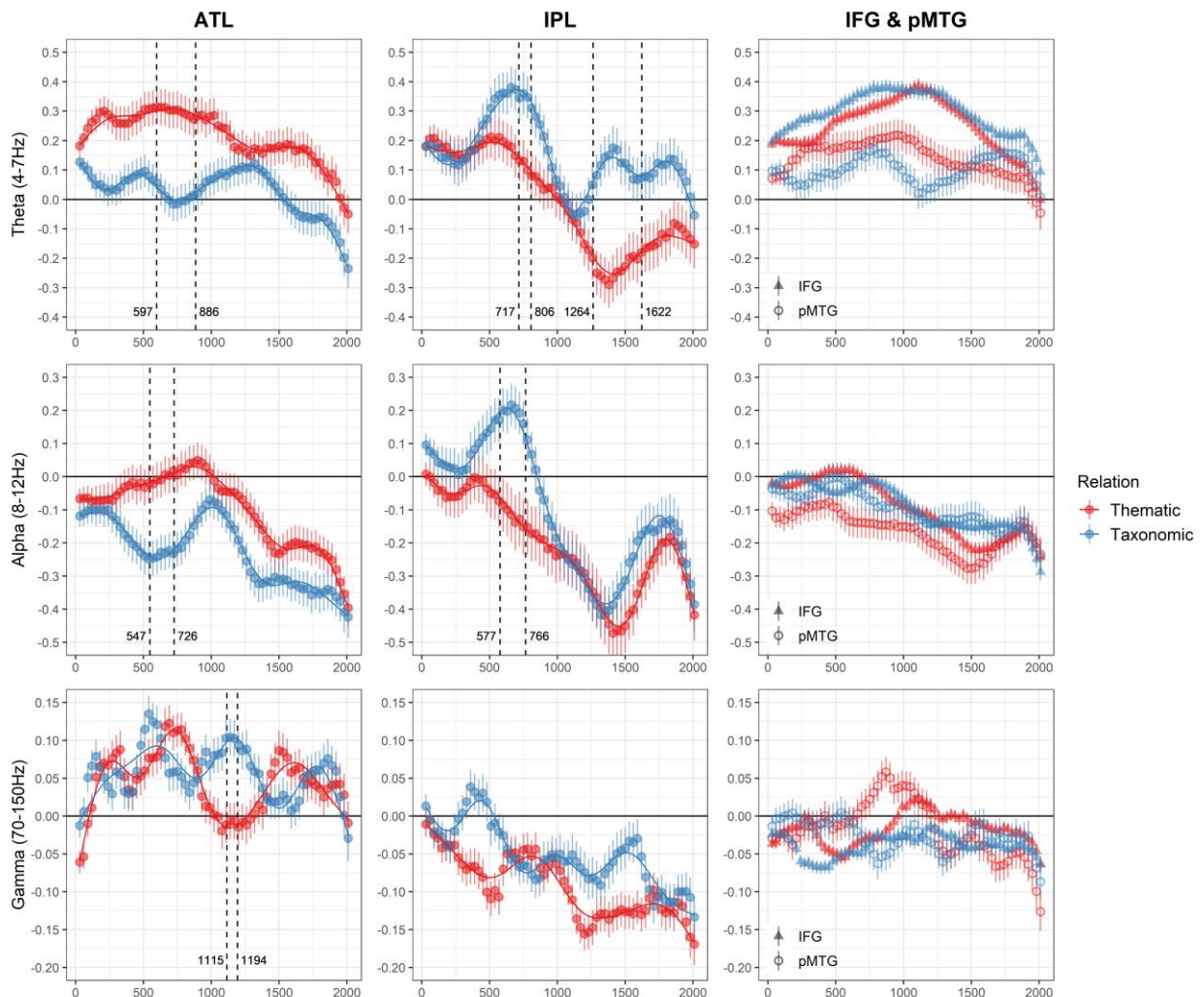


Figure 2. The time course of spectral power for the theta (top row), alpha (middle row), and high gamma (bottom row) frequency bands for ATL (left column), IPL (middle column), and IFG and pMTG (right column). For the semantic control regions shown in the right column, IFG data are plotted with filled triangles and pMTG data are plotted with open circles. Time (0-2000ms post trial onset) is shown on the x-axis and the log transformed signal is shown on the y-axis. Thematic relation trials are shown in red, taxonomic trials are shown in blue, and the time windows with statistically significant differences between conditions are marked by dashed vertical lines.

4. Discussion

Two opposing theoretical accounts of semantic cognition were examined using intracranial EEG. These accounts make different predictions about the functional specialization for taxonomic and

^d Diagnostic plots indicated that the distribution of residuals was heavy-tailed in the gamma models, so these models were re-run using a scaled T distribution. With these models, the condition effect in ATL was no longer significant.

thematic knowledge. The single-hub account predicts equal responses for taxonomic and thematic relations in ATL and no evidence of specialization within IPL. Conversely, the dual-hub account predicts stronger response in ATL for taxonomic relations and in IPL for thematic relations. Differences in the relative reliance on a broader semantic control network were also investigated by examining responses in IFG and pMTG. Using prior norming, behavioural, and psychophysiological evidence (Geller et al., 2019; Landrigan & Mirman, 2016), the stimuli were designed to minimise and match control demands for the taxonomic and thematic semantic relation conditions, which presented an opportunity to test whether thematic relations inherently recruit the semantic control system. Based on prior intracranial EEG studies, stronger neural response was operationalised as reduced theta and alpha power and increased high gamma power (Herweg et al., 2020; Klimesch, 2012; Lachaux et al., 2007).

The ATL and IPL showed differential responsiveness to taxonomic and thematic relations in low frequency bands, where reduced spectral power is associated with task engagement and memory retrieval (Drijvers et al., 2018; Herweg et al., 2020; Klimesch, 2012). In ATL, the taxonomic condition response was significantly reduced relative to the thematic condition response from 597 to 886ms in the theta band and from 547 to 726ms in the alpha band. The opposite pattern was seen in IPL, with reduced theta power on thematic compared to taxonomic trials from 717 to 806ms and again from 1264 to 1622ms and reduced alpha power from 577 to 766ms. These results are consistent with the dual-hub prediction of greater ATL engagement in retrieving taxonomic relations and greater IPL engagement in retrieving thematic relations.

The relatively symmetric functional specialisation observed in this study is likely a product of the matched taxonomic and thematic stimuli and task, combined with the high spatial and temporal resolution of sEEG. Other studies that showed converging evidence of functional specialisation have not always found such symmetric effects. For instance, in picture naming, participants usually make more taxonomic errors than thematic errors, possibly because visual features – which tend to be shared among taxonomically-related items – are more salient in a picture-based task. The lesion-symptom mapping analyses in Schwartz et al. (2011) showed that increased rate of taxonomic errors *controlling for rate of thematic errors* was associated with ATL damage and increased rate of thematic errors *controlling for rate of taxonomic errors* was associated with IPL damage. That is, although all participants made more taxonomic errors than thematic errors, the magnitude of that difference depended on the lesion location.

The timing of the observed effect may also be an important consideration when situating the present results in the broader literature. The specialization observed here was relatively early, transient, and primarily in the lower frequencies – the ATL and IPL hubs showed different degrees of suppression of low frequency (theta and alpha band) oscillations early after trial onset, but then seemed to work cooperatively to retrieve taxonomic and thematic relations. Studies using fMRI may not have been able to capture this transient dissociation given the lack of temporal resolution and may have been primarily capturing high gamma band power, which is more strongly associated with the BOLD signal. For example, a recent fMRI study using representational similarity analysis found that representational patterns in IPL showed approximately equal taxonomic and thematic similarity, while representational patterns in ATL showed much stronger taxonomic similarity than thematic similarity (i.e., Xu et al., 2018). Although both the Xu et al. fMRI study and the current sEEG study provide very clear evidence consistent with the dual-hub account, they do so on the basis of rather different neural signatures.

Alpha and theta suppression were most prominent in both ATL and IPL relatively early in the time course, approximately 550-750ms after trial onset. The time course of activation was largely

consistent across the low frequency bands and condition differences occurred at approximately the same time within ATL and IPL. It is important to note that the statistically significant time windows should not be interpreted as qualitatively distinct stages; they identify time points that passed a statistical significance threshold, thus highlighting the time points where the differences were strongest. However, the stimulus-evoked responses evolve gradually, so the adjacent time points outside of the identified windows likely fall just below the statistical threshold. These results do indicate that the differential response is a transient aspect that occurs early in semantic retrieval. Methods with coarser temporal resolution (such as fMRI) would be unlikely to capture these transient differences which underscores the value of using intracranial methods to enhance current neurobiological models of semantic cognition. Across most of the time course, ATL and IPL responded similarly on taxonomic and thematic trials, suggesting substantial coordinated processing between these semantic hubs. Although neither the single-hub nor dual-hub account make any particular claims about the time course of activation, the transient differential response conflicts with the single-hub CSC framework prediction that ATL and IPL should respond equally to taxonomic and thematic relations under conditions requiring minimal semantic control. The stimuli and task were specifically designed to minimise and match semantic control demands and the lack of condition differences in IFG and pMTG suggest that this was successful. It is important to note that electrode coverage within the most posterior portion of pMTG was limited in this sample of participants, but no condition effect was observed in either semantic control region. Retrieval of strongly related taxonomic and thematic relations did not exert differential demands on the semantic control system.

Within the high gamma band, the taxonomic condition response was significantly higher than the thematic condition response from 1115 to 1194ms in ATL, but no condition differences were seen in either IPL, IFG, or pMTG. Taken together with the theta and alpha band, these results align with the spectral tilt phenomenon reported in studies of human memory wherein decreased power is observed in lower frequency bands (i.e., theta and alpha) with corresponding power increases seen in higher frequencies (> 30 Hz) (Herweg et al., 2020). Although the time window is relatively brief, this is consistent with the ATL preferentially processing taxonomic relations, though a complementary tilt for thematic relations was not found in IPL and the low-frequency ATL response appears to be more robust. Given the known correspondence between high gamma band power and the BOLD response (Engell et al., 2012; Lachaux et al., 2007), this result may explain the mixed reports of ATL and IPL involvement in fMRI studies investigating taxonomic and thematic relations (Geng & Schnur, 2016; Jackson, Hoffman, Pobric, & Lambon Ralph, 2015; Xu et al., 2018).

Previous scalp EEG and MEG studies have attempted to isolate the time course of activation associated with processing taxonomic and thematic relations, although without the spatial resolution provided by intracranial recording. Many of these studies have reported key differences in processing of taxonomic compared to thematic relations. For instance, taxonomic and thematic relations were found to produce distinguishably different N400 amplitudes (Honke, Kurtz, & Laszlo, 2020), P600 amplitudes were significantly larger for taxonomic compared to thematic items (Savic, Savic, & Kovic, 2017), and a larger frontal P600 response was observed for taxonomic compared to thematic relations (Chen et al., 2013). One scalp EEG study reported increased theta power in right frontal regions for thematic relations and increased alpha power over parietal areas for taxonomic relations (Maguire, Brier, & Ferree, 2010) which is largely consistent with the alpha and theta suppression observed in the current study. It is important to note, however, that scalp EEG and MEG may not be directly comparable to intracranial EEG: these methods consistently produce discrepant results, suggesting that they are capturing different properties of the frequency band. In particular, intracranial recordings capture oscillations in local field potentials that are interpreted as general

increases in power when coarsely recorded at the scalp (Herweg et al., 2020). The results of the present study highlight the applicability and potential of intracranial EEG to further current understanding of human cognition.

The functional specialization observed in this study is consistent with the “architectural specialization” hypothesis proposed by Mirman et al. (2017) in which the neural architecture of semantic cognition is divided according to the differential demands of identification and prediction. Identification and categorization of concepts based on features captures taxonomic relations whereas prediction based on temporal regularities of events captures thematic relations (for a related computational implementation see Hoffman, McClelland, & Lambon Ralph, 2017). The present data suggest that ATL is specialized for identification, categorization, and taxonomic relations (consistent with extensive prior research, e.g., Lambon Ralph et al., 2017; Patterson et al., 2007), while IPL is specialized for prediction and thematic relations (e.g., Matchin, Hammerly, & Lau, 2017; van Kemenade, Arikan, Kircher, & Straube, 2017; Xu et al., 2018). The emphasis on prediction is consistent with previous evidence indicating that thematic relations are asymmetrical. Semantic retrieval of causal relations (one kind of thematic relations) is facilitated when they are presented in cause-effect order (Fenker, Waldmann, & Holyoak, 2005). Regularities in sequences of how concepts co-occur in an event may drive asymmetries in semantic association that have been demonstrated in semantic priming (Hutchison, 2002). Although not explicitly tested in this study, altering the direction of thematic (but not taxonomic) relations may result in varied IPL involvement due to increased prediction demands. The transient differential response observed in the present experiment suggests that, in a general semantic relation judgement task with randomly interspersed taxonomic and thematic trials, both hubs were substantively engaged on each trial; however, on taxonomic trials, a coherent relation was activated in ATL, whereas on thematic trials, the coherent relation was activated in IPL.

5. Conclusion

Intracranial EEG was used to investigate the spatio-temporal dynamics of semantic cognition. A neural dissociation in response to semantic relation type was observed in the two major semantic hubs. Early decreases in low frequency power were stronger for taxonomic relations in ATL and for thematic relations in IPL. No difference was found in either semantic control region suggesting equal semantic control demands for strongly related taxonomic and thematic relations. These results are consistent with a dual-hub account in which ATL is functionally specialized for taxonomic relations and IPL for thematic relations, although the transience of the effect suggests close coordination between these two hubs.

Open Practices Statement

Transparency statement: No part of the study procedures or analyses were pre-registered prior to the research being conducted. We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. The preprocessed data and all code needed to run analyses are available on OSF (<https://osf.io/xtfah/>). The conditions of our ethics approval do not permit public archiving of the raw signal data associated with this study. Readers seeking access to the data should contact Dr. Dan Mirman (dan@danmirman.org). Access will be granted to named individuals in accordance with ethical procedures governing the reuse of sensitive data, completion of a formal data sharing agreement, and approval by the ethics committee.

Acknowledgements

The investigators thank Diana Pizarro for developing the recording device used in this study. This development was supported by the National Science Foundation EPSCoR Research Infrastructure Improvement Program: Track-2 Focused EPSCoR Collaborations (RII Track-2 FEC) under award number 1632891 (UAB PI: J.P.S.). The data were collected at the UAB Epilepsy Center while M.T., J.G., and D.M. were in the Department of Psychology, University of Alabama at Birmingham. We thank the patients who generously gave their time to participate in this study.

Author Contributions

Conceptualisation, D.M. and J.P.S.; Methodology, M.T. and J.G.; Investigation, M.T. and J.P.S.; Software, M.T. and D.M.; Data Curation, M.T.; Formal Analysis, M.T., D.M., J.G.; Writing – Original Draft, M.T.; Writing – Review & Editing, M.T., J.G., J.P.S., and D.M.; Supervision, D.M. and J.P.S.

Declaration of Interests

The authors declare no competing interests.

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Supplemental Table 1

Participant Electrode Coverage

<i>Participant</i>	ATL	IPL	IFG	pMTG	Total
01	9	4	6	4	23
02	0	0	8	0	8
03	0	0	11	3	14
04	0	0	11	7	18
05	0	8	6	2	16
06	0	0	7	4	11
07	5	0	4	9	18
08	0	3	12	1	16
09	0	0	4	6	10
10	4	6	0	11	21
11	5	3	3	3	14
12	9	0	5	0	14
13	7	1	10	5	23
14	0	0	2	0	2
15	7	0	12	1	20
16	10	0	9	4	23
17	0	0	6	2	8

Note. Total refers to the number of electrode channels within one of the regions of interest for each participant. ATL, anterior temporal lobe; IPL, inferior parietal lobule; IFG, inferior frontal gyrus; pMTG, posterior middle temporal gyrus.

Supplemental Table 2

Task Stimuli

Taxonomic Pairs (n=16)	Thematic Pairs (n=16)	Unrelated Pairs (n=64)			
ale – cola	blade – armour	alien – scorpion	dune – queen	mountain – chip	spinach – gun
bucket – vase	drizzle – cloud	arrow – tooth	earring – gravy	note – bull	steel – medicine
chicken – owl	forest – trail	balloon – mustard	envelope – lime	pasta – ink	sword – napkin
dentist – surgeon	gown – corsage	block – pilot	foundation – towel	patio – knight	tail – tire
dinner – breakfast	ketchup – burger	bread – chain	gas – magazine	pin – kitty	thorn – fan
jug – urn	light – star	bulb – dog	glove – pretzel	planet – container	thunder – folder
juice – lager	map – route	cable – ocean	grill – pyramid	plantation – pan	toilet – pendant
lamb – cow	monkey – banana	candy – pebble	hair – spatula	plate – basketball	torch – potato
lunch – snack	navy – anchor	canoe – jester	hoop – resume	plug – hat	tricycle – river
otter – rat	padlock – diary	case – web	island – shoe	purse – lobster	viper – stylus
pail – pot	palm – coconut	cave – basket	jackal – sink	reef – building	vulture – page
president – monarch	shovel – sandbox	cheetah – candle	kayak – cheese	rod – mayonnaise	wallet – plant
seal – beaver	soysauce – sushi	computer – radish	lid – crab	rubber – turtle	whiskey – pillow
skunk – rabbit	sugar – tea	cougar – bridge	lightning – cane	salsa – air	wife – football
taxi – airplane	trench – bayonet	cup – weapon	lion – glass	shampoo – cord	wine – grass
yarn – floss	tv – couch	dirt – cake	moth – base	skeleton – flower	yogurt – sail

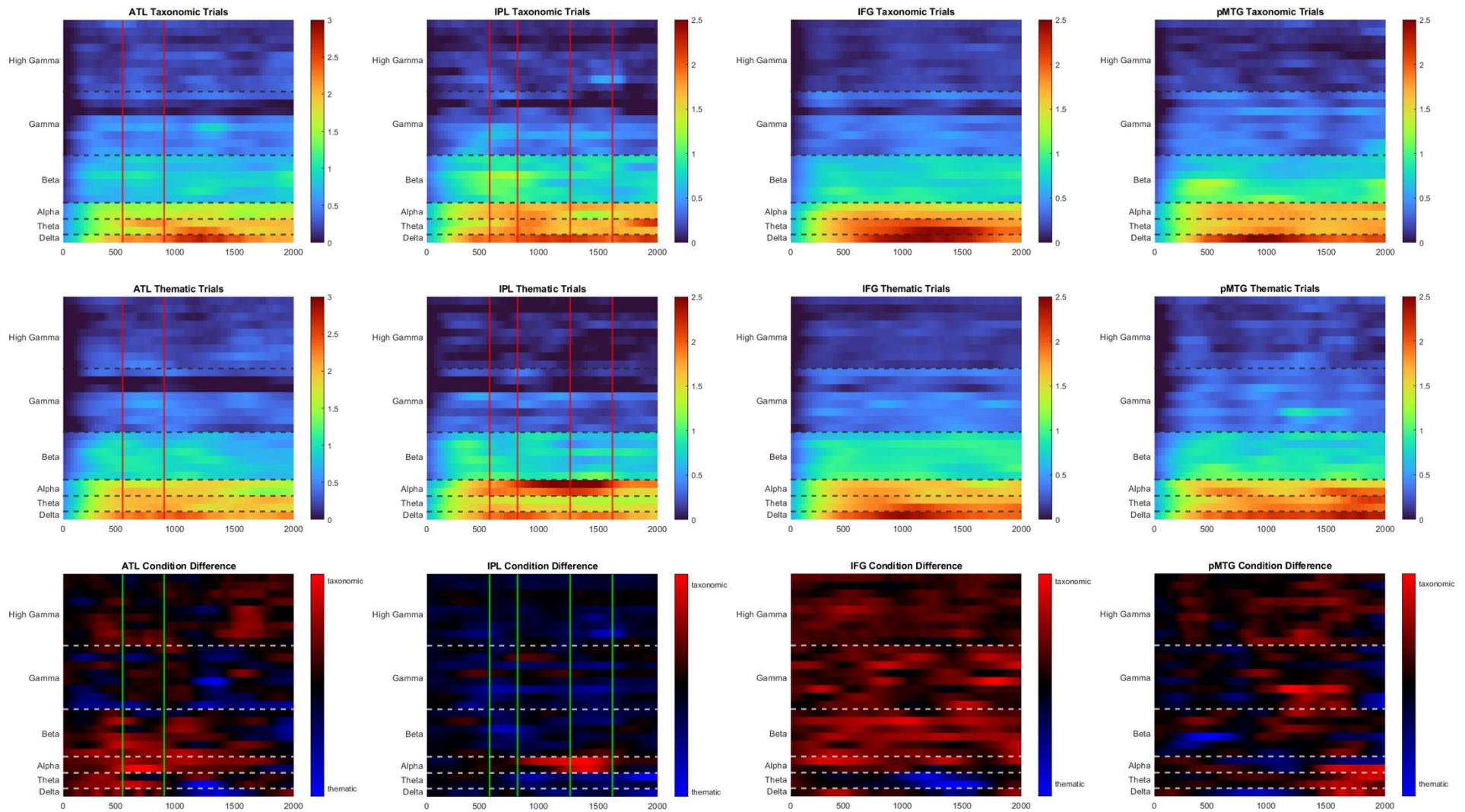
Note. The full task included both strongly (n=32) and weakly (n=32) related taxonomic and thematic word pairs and an equal number of unrelated, filler pairs (n=64). Only the strongly related taxonomic and thematic pairs are shown here. The weakly related pairs are available on the project OSF page, but were not analysed in the present manuscript. All unrelated, filler pairs are listed and shown shaded in grey.

Supplemental Table 3

Model Results

	Trial Type Est(SD); <i>t</i> -value	s(Time) edf(rdf); <i>F</i> -value	s(Time):Them edf(rdf); <i>F</i> -value	s(Time):Tax edf(rdf); <i>F</i> -value	fs(Time, Electrode) edf(rdf); <i>F</i> -value	re(subj_word) edf(rdf); <i>F</i> -value
Theta						
ATL	-0.17(0.10); -1.76 [†]	0.01(0.01); 0.03	6.69(7.49); 2.84**	8.25(8.63); 9.03***	371.66(560); 3.33***	151.40(187); 5.80***
IPL	0.19(0.10); 1.84 [†]	0.00(0.00); 0.00	6.62(7.42); 2.14*	8.61(8.83); 16.42***	154.03(249); 5.12***	108.28(148); 3.80***
IFG	0.09(0.06); 1.64	3.43(3.82); 0.35	6.99(7.75); 3.69**	3.21(3.63); 1.18	808.68(1159); 3.20***	295.29(400); 3.64***
pMTG	-0.01(0.08); -0.08	3.09(3.63); 0.33	1.00(1.01); 2.69	7.50(8.44); 7.16***	461.23(618); 3.82***	254.77(347); 3.64***
Alpha						
ATL	-0.12(0.09); -1.31	2.45(2.57); 0.02	6.02 (6.61); 1.39	7.51(7.97); 3.94***	407.60(559); 4.55***	152.00(187); 6.03***
IPL	0.10(0.10); 0.95	6.54(6.67); 2.57*	5.30(5.60); 0.37	5.94(6.27); 1.53	169.31(248); 4.31***	112.50(148); 5.26***
IFG	0.01(0.05); 0.22	1.06(1.06); 0.00	8.34(8.62); 9.21***	7.98(8.38); 6.49***	814.16(1160); 3.32***	311.17(399); 4.70***
pMTG	0.04(0.07); 0.51	5.47(6.01); 2.04 [†]	7.11(8.25); 5.18***	1.01(1.01); 18.45***	446.03(618); 4.85***	262.84(348); 4.15***
Gamma						
ATL	0.02(0.04); 0.45	1.01(1.01); 0.00	8.52(8.95); 15.25***	8.44(8.93); 10.41***	62.84(558); 0.42***	165.71(186); 8.83***
IPL	0.04(0.03); 1.21	1.00(1.00); 0.00	7.17(8.36); 3.48***	8.33(8.90); 5.02***	23.98(248); 0.33***	112.34(148); 4.53***
IFG	-0.03(0.02); -1.72 [†]	7.47(7.75); 13.46***	3.29(4.02); 0.21	3.19(3.89); 0.14	131.41(1159); 0.34***	326.64(400); 5.21***
pMTG	-0.01(0.03); -0.30	3.36(3.95); 0.54	6.05(7.03); 2.71**	4.61(5.46); 1.69	29.95(619); 0.15***	274.84(349); 4.69***

Note. Parameter estimates for each model (rows). The random effects are shaded in grey. edf, estimated degrees of freedom (values close to 1 indicate a linear relationship); rdf, reference degrees of freedom; fs, factor smooth; re, random effect (intercept); ATL, anterior temporal lobe; IPL, inferior parietal lobule; IFG, inferior frontal gyrus; pMTG, posterior middle temporal gyrus. Model specification: $bam(\log(\text{signal}) \sim \text{Trial_Type} + s(\text{Time}) + s(\text{Time}, \text{by}=\text{Trial_Type}) + s(\text{Time}, \text{Electrode}, \text{bs}=\text{"fs"}) + s(\text{subj_word}, \text{bs}=\text{"re"}))$. [†] $p < .09$, * $p < .05$, ** $p < .01$, *** $p < .001$.



Supplemental Figure 1. Time-frequency plots. Frequency bands are indicated with dashed horizontal lines and the windows of significant condition

differences within the theta and alpha band are indicated with vertical green or red lines. Taxonomic (top row), thematic (middle row), and the condition difference plot (bottom row) are presented for ATL, IPL, IFG, and pMTG separately. For the condition difference figures, red indicates greater power for taxonomic trials and blue indicates greater power for thematic trials.