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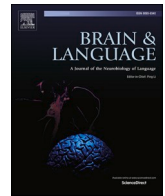
Phase synchronization during the processing of taxonomic and thematic relations

Erica Adezati [a,1], Xianqing Liu [a,1], Junhua Ding [a], Melissa Thye [a], Jerzy P. Szaflarski [b], Daniel Mirman [a,*]

[a] Department of Psychology, University of Edinburgh, Edinburgh, UK
[b] Department of Neurology and the University of Alabama at Birmingham (UAB) Epilepsy Center, University of Alabama at Birmingham, Birmingham, AL 35294, USA

ABSTRACT

Semantic relations include "taxonomic" relations based on shared features and "thematic" relations based on co-occurrence in events. The "dual-hub" account proposes that the anterior temporal lobe (ATL) is functionally specialized for taxonomic relations and the inferior parietal lobule (IPL) for thematic relations. This study examined this claim by analyzing the intra- and inter-region phase synchronization of intracranial EEG data from electrodes in the ATL, IPL, and two subregions of the semantic control network: left inferior frontal gyrus (IFG) and posterior middle temporal gyrus (pMTG). Ten participants with epilepsy completed a semantic relatedness judgment task during intracranial EEG recording and had electrodes in at least one hub and at least one semantic control region. Theta band phase synchronization was partially consistent with the dual-hub account: synchronization between the ATL and IFG/pMTG increased when processing taxonomic relations, and synchronization within the IPL and between IPL and pMTG increased when processing thematic relations.

1. Introduction

Semantic memory refers to the interconnected store of conceptual knowledge of objects, people, and facts (Patterson et al., 2007). It allows us to interpret word meanings, recognize objects and entities, interact with them, and have expectations about them (McRae & Jones, 2013). There are different types of semantic relations, including "taxonomic" and "thematic" relations. Taxonomic relations group concepts, objects and people on the basis of shared features (e.g., cola-ale), which support inferential generalisations concerning exemplars of the same category (Estes et al., 2011). Thematic relations, on the other hand, group concepts, objects and people on the basis of their participation in the same scenario or event (e.g., couch-television), including, for instance, causal, temporal and functional relations (Estes et al., 2011). Research suggests that taxonomic and thematic semantic knowledge may rely on separate neural systems (Estes et al., 2011; Mirman et al., 2017). Prior studies have reported both spatial and temporal dissociations, though the evidence is mixed and sometimes contradictory.

The spatial dissociation has focused on the roles of the anterior temporal lobes (ATL) and the left inferior parietal lobule (IPL). The ATL is a well-established hub for integrating information from multimodal spokes to form semantic representations (Lambon Ralph et al., 2017; Patterson et al., 2007) that might be specialised for taxonomic relations. The IPL is also a transmodal convergence zone for semantic and episodic memory (Binder & Desai, 2011) that might be specialised for thematic knowledge. This 'dual-hub' account is supported by evidence using different approaches and cohorts (for a review see Mirman et al., 2017): lesion-symptom mapping in post-stroke aphasia, fMRI and MEG studies in neurotypical participants, and intracranial EEG recordings in patients with treatment-refractory epilepsy (Schwartz et al., 2011; Thye et al., 2021; Xu et al., 2018). However, some studies find either no dissociation (e.g., Jackson et al., 2015) or a partial dissociation, such as IPL specialisation for thematic relations but ATL showing approximately equal sensitivity to both kinds of relations (e.g., Zhang et al., 2023).

The temporal dissociation is even more mixed, in part because timing of semantic processing is more strongly influenced by task demands and strength of semantic relationship than by type of semantic relationship (for a review see Mirman et al., 2017). Nevertheless, ERP studies using scalp EEG have found that the N400 is more negative for taxonomic relations compared with thematic relations (Anderson et al., 2022;

Maguire et al., 2010), while P600 is stronger for thematic relations than taxonomic relations (Chen et al., 2013, 2014). MEG studies have found that this functional specialisation pattern emerges 250–600 ms after stimulus onset (Lewis et al., 2015; Teige et al., 2019). Specifically, the functional specialisation of the IPL for thematic relations emerged earlier (250–400 ms) than that of the ATL for taxonomic relations (400–600 ms). Our prior intracranial EEG study found that the timing of IPL specialisation for thematic relations and ATL specialisation for taxonomic relations was similar, with effects approximately 550–800 ms and again 1250–1600 ms after stimulus onset (Thye et al., 2021).

These hubs are critical for semantic cognition, but effective communication within and between brain networks is necessary for most cognitive processes (Cohen & D'Esposito, 2016). Specifically, semantic processing requires retrieving the particular information that is relevant to the context or task in question and ignoring the irrelevant information (Lambon Ralph et al., 2017). Such "semantic control" functions are thought to be supported by the inferior frontal gyrus (IFG) and posterior middle temporal gyrus (pMTG), as described in the Controlled Semantic Cognition (CSC) model (Jefferies et al., 2020; Lambon Ralph et al., 2017) and supported by a substantial literature using different methods, including fMRI, TMS, and neuropsychological tests (Jefferies & Lambon Ralph, 2006; Noonan et al., 2013; Whitney et al., 2011). Furthermore, some evidence of functional specialisation for taxonomic vs thematic relations can be explained by differential reliance on semantic control regions in coordination with a single ATL hub (Thompson et al., 2017; M. Zhang et al., 2021).

In sum, the semantic hubs and control system must coordinate activity during semantic cognition tasks, though this has not been investigated directly, partly because typical cognitive neuroscience methods (e.g., fMRI and scalp EEG) do not have the combination of spatial and temporal resolution needed to capture the rapid, transient coordination between nearby brain regions that would be involved in identifying semantic relations.

1.1. The current study

In this study, we examined connectivity between semantic hubs and semantic control regions using stereoelectroencephalography (sEEG) recordings from electrodes implanted directly in the brain, which provide finer spatial and temporal resolution than other methods (e.g., fMRI and scalp EEG). In our prior sEEG work (Thye et al., 2021), we found that ATL and IPL showed functional specialization for taxonomic and thematic relations (respectively) that were reflected in lower frequency band power (theta and alpha bands) approximately 550–800 ms after stimulus onset, and IPL showed preferential response to thematic relations in the theta band again 1250–1600 ms after stimulus onset. Semantic control regions (IFG and pMTG) did not show such specialisation. Here, we further examine those data for evidence of increased synchronization of activity within the ATL and IPL semantic hubs and between the hubs and semantic control regions.

Phase synchronization of oscillating EEG signals is a fundamental neural pattern that indicates information communication and functional coordination of neural activity, which is considered relevant for many cognitive processes, such as working memory, long-term memory and cognitive control (Beppi et al., 2020; Daume et al., 2017; Marzetti et al., 2019). According to the classic theory of 'communication through coherence', only coherently oscillating neural assemblies can effectively transfer information (Fries, 2005). Two synchronized neural groups will have a higher probability to generate action potentials on each other or another group and induce long-term potentiation for spike timing-dependent plasticity (Fell & Axmacher, 2011). Specifically, local synchronization within the memory system plays a crucial role in memory formation, storage and retrieval. Remote synchronization between memory and executive function modules is associated with top-down control, including attention, monitoring, and inhibition for memory tasks (Beppi et al., 2020; Daume et al., 2017). This index successfully

predicts working memory capacity and can distinguish remembered and forgotten words (Fell & Axmacher, 2011; Marzetti et al., 2019).

The present study examined the phase synchronization patterns intra- and inter-brain regions during processing of taxonomic and thematic relations. First, intra-region synchronization was explored among electrodes within left ATL, IPL, IFG and pMTG. The dual-hub account predicts that phase synchronization for ATL-ATL electrodes should be higher during taxonomic trials than during thematic trials, and vice versa for IPL-IPL electrodes. Because the conditions were matched on overall difficulty, taxonomic and thematic trials should evoke approximately equal intra-region phase synchronization among electrodes within semantic control regions (pMTG and IFG). Second, we explored the inter-region synchronization between semantic representation hubs and semantic control regions during processing of taxonomic and thematic relations. The dual-hub account predicts higher phase synchronization between the ATL electrodes and electrodes in semantic control regions (pMTG and IFG) during taxonomic trials compared to thematic trials, and vice versa for phase synchronization between the IPL electrodes and electrodes in semantic control regions. That is, the dual-hub account predicts that IPL phase synchronization (within IPL and between IPL and IFG/pMTG) will increase over time on thematic trials more than on taxonomic trials; conversely, ATL phase synchronization (within ATL and between ATL and IFG/pMTG) will increase over time on taxonomic trials more than on thematic trials.

Finally, in the exploratory analyses, we tested whether sEEG synchronization beyond ATL, IPL, IFG and pMTG also shows specialization for thematic relations. This is based on a recent study (Blackett et al., 2022) that used connectome-based lesion-symptom mapping (CLSM) in post-stroke aphasia to identify two white matter connections that were specifically associated with processing thematic relations: (1) inferior temporal gyrus (ITG) to insula and (2) middle temporal pole (MTP) to posterior cingulate gyrus (PCG). If the synchronization between these region pairs is specialized for thematic relations, this will provide further evidence of functional specialization for taxonomic vs thematic relations within the brain networks that support semantic cognition.

2. Methods

2.1. Participants

Thirty-one patients with treatment-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 h 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 location 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 (at least one semantic hub and one semantic control region; n = 13). Exclusion criteria were established prior to data analysis. The final sample for analysis consisted of 10 participants. The demographic and neuropsychological information is provided in Table 1. The study was carried out following protocols approved by the Institutional Review Board at the University of Alabama at Birmingham and the PPLS Research Ethics panel (253–2122/1).

Table 1
Participant information.

	N	Mean (SD)		Range
Age (years)	10	33.80 (7.77)		24–44
Sex (Male: Female)	3:7			
Full Scale IQ	9	93.67 (21.08)		61–129
Verbal IQ	10	100.20 (20.56)		63–130
Semantic Fluency	9	17.78 (5.29)		9–24
Accuracy (%)				
Taxonomic Trials	10	82.5 (11.3)		68.8–100
Thematic Trials	10	86.2 (11.3)		62.5–100
Response Time (s)				
Taxonomic Trials	10	3.84 (1.40)		1.81–6.26
Thematic Trials	10	3.62 (1.51)		1.59–6.60
	N	No. Channels	Coverage Mean (Range)	No. Channel Pairs
ATL-ATL	8	56	7 (4–10)	185
IPL-IPL	5	24	5 (3–8)	55
IFG-IFG	9	70	8 (3–15)	301
pMTG-pMTG	7	37	5 (2–11)	113
ATL-IFG	7			378
ATL-pMTG	7			215
IPL-IFG	5			136
IPL-pMTG	6			114

Note. N, number of participants; SD, standard deviation of the mean; No., number; 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.

2.2. Materials

Participants completed a semantic relatedness judgment task used in a previous study with neurologically typical participants (Geller et al., 2019). Related 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). Only the strongly related trials were analyzed in the current study because they have a clear contrast between the two relations (rating difference for taxonomic trials: M = 2.1, SD = 0.3; thematic trials: M = -2.4; SD = 0.4). These trials were previously found in 60 healthy participants to be matched in terms of control demands based on response times, accuracy, and the task-evoked pupillary responses, which is a psychophysiological measure of cognitive effort (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 neighborhood size.

2.3. Procedure

Participants completed an approximately 1-hour testing session consisting of four language tasks during continuous sEEG monitoring. Intracranial video-EEG from an array of multicontact 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 rate 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 8 practice trials prior to beginning each task. During the semantic relatedness task, two words appeared on the screen each

with a physical size of 1.69 cm 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 related trials, 16 in each condition, and 64 unrelated filler trials) were presented until the participant provided an answer with an inter-trial interval of 2000 ms during which participants saw a fixation cross. Trials were presented in 8 discrete blocks and participants were given a break after each block. Trial onset signals from the experiment 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 Pre-processing

Participant pre-operative MRI scans were processed through FreeSurfer (Dale et al., 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 center of the visible artifact 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 et al., 2010) and referenced to standard atlases using code adapted from (Stolk et al., 2018). Electrode locations were visualized by generating a 3 mm sphere around each normalized coordinate using AFNI (Cox, 1996).

Signal data were pre-processed in MATLAB 2021a (MATLAB, 2021) using the signal processing and FieldTrip toolboxes. Data were segmented into 2500 ms windows capturing the trial and baseline period (500 ms). Trials were demeaned and line noise around 60 Hz (and its 2nd and 3rd order harmonics) was attenuated with a notch filter. Data were visually inspected, and channels with consistent artifactual fluctuations across trials were removed (n = 25). An objective and automated artifact rejection algorithm (Piai et al., 2016) was run on the z-transformed data (threshold = 7), and trials that contained excessively large amplitudes were excluded from analysis (4.6% of trials). Of note, we did not inspect the EEG tracings for epileptiform discharges. Manual epileptiform discharges removal is performed commonly, but it is not universal as a pre-processing step (Ammanuel et al., 2020). It has poor inter-rater agreement even among highly trained individuals (Barkmeier et al., 2012) and formal comparison of manual, automated or no removal of epileptiform discharges found no clear effect of either of those approaches on statistical power (Meisler et al., 2019). Therefore, we opted for maximizing replicability and removal of only reliably-detectable artifacts. The data were downsampled to 500 Hz 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 (4–7 Hz), the alpha band (8–12 Hz), and high frequency broadband (HFB; i.e. high gamma band; 70–150 Hz).

The Hilbert transform was applied to compute the phase of signal oscillation within each of the extracted frequency bands for each electrode. Phase synchronization between pairs of electrode channels was quantified using phase locking value (PLV) for every 100 ms time bin within the onset-locked 2500 ms time window (Lachaux et al., 1999):

$$PLV_f = \frac{1}{N} \left| \sum_{n=1}^{N} e^{i\left(\theta_x(n) - \theta_y(n)\right)} \right|$$

where *f* is the frequency band, *N* is the number of time points, and $\theta_x(n)$ and $\theta_y(n)$ are phase angles from electrodes *x* and *y*, respectively, at time point *n*. The PLVs were then smoothed by overlapping sliding windows of 250 ms every 30 ms and baseline corrected by calculating the percent change from the 300 ms prior to the trial onset.

Data were recorded from a total of 707 cortical electrode channels for the 10 participants included in the analysis, of which 519 were excluded from analyses due to excessive artifacts or placement outside

of the regions of interest (ROIs). The ROIs were derived using the cortical parcellation of several atlases because the critical functional regions are not clearly defined in any single anatomical atlas, although there was significant overlap in the region definitions across atlases. The left ATL region was comprised of the left middle and superior temporal pole regions within the AAL atlas (Tzourio-Mazoyer et al., 2002), the left temporal pole region within the Harvard-Oxford atlas, and the left temporal pole region within the Destrieux atlas (defined in participant native space) (Destrieux et al., 2010). The left IPL region was comprised of the left supramarginal and angular gyri regions within the AAL atlas and the left supramarginal region within the Desikan-Killiany atlas (defined in participant native space) (Desikan et al., 2006). The left IFG region was comprised of the left orbital, triangular, and opercular parts of the inferior frontal gyrus in the AAL atlas, and the left 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 left temporo-occipital part of the middle temporal gyrus within the Harvard-Oxford atlas. Fig. 1 (left) shows the electrode coverage across participants in these four regions of interest.

2.5. Statistical analysis

Filler, weakly related, inaccurate (15.6%), and slow response (RT > 10 s; 8.8%) trials were removed prior to analysis. To test whether response behavioral performance differed across taxonomic and thematic conditions, logistic and linear multilevel models were built to fit the observed accuracy and reaction time, respectively. Both models contained a fixed effect of relation type (taxonomic vs. thematic), and crossed random effects of participants and trials. The phase synchronization analyses were conducted using a 2 s window starting at trial onset. This window was selected because (1) neural signatures of semantic processing typically emerge within the first 1–2 s after stimulus presentation, even if the response occurs somewhat later, (2) there was a broad range of response times across trials, but at 2 s, almost all trials had not yet been terminated by a response so we can (more) reasonably assume that this time window reflects processing of the presented stimuli rather than other post-response or between-trial cognitive processes, and (3) it is consistent with our prior study based on this data set (Thye et al., 2021), which used a 2-second window and observed effects approximately 550–800 ms and again 1250–1600 ms after stimulus onset. General PLV differences between relation types and their time course were analyzed using linear mixed effect models. A linear mixed model predicting the PLV within each frequency band was run for each ROI pair with fixed effects of relation type, time and their interaction, and random intercepts for participants and trials, and random intercepts

and slopes for electrode pairs. That is, we modeled PLV observations as nested within electrode pairs (random effects of electrode pair) and participants (random effects of participants) with crossed nesting by word pair (random effects of trial), and estimated group-level (fixed) effects of relation type over time in each ROI pair. Individual differences across participants, trials and electrodes were thus captured by the random effects within the model specification. All models were estimated using the lme4 package (Bates et al., 2015). The degrees of freedom for the coefficient tests were estimated via Satterthwaite's method using the lmerTest package (Kuznetsova et al., 2017). Three frequency bands (theta, alpha, HFB) were considered independent tests (i.e., the dual-hub hypothesis could be supported in any one of the three frequency bands), thus a Bonferroni correction was applied by dividing the standard alpha ($\alpha = 0.05$) by 3, resulting in a corrected significance level of $\alpha = 0.017$.

The PLV values of theta and alpha bands were not normally distributed. Thus, they were further transformed by the Box-Cox transformation. The parameter of the transformation was specifically optimized for each model and the model refit for these two frequency bands as a validation analysis. In addition, to control for the impact of RT, RT was included as a fixed effect and by-participants random slope. To gain further insights into the timing of the effects, we repeated the analyses with progressively longer time windows: 0–500 ms, 0–1000 ms, 0–1500 ms (supplementing our originally planned analyses of the full 0–2000 ms time window).
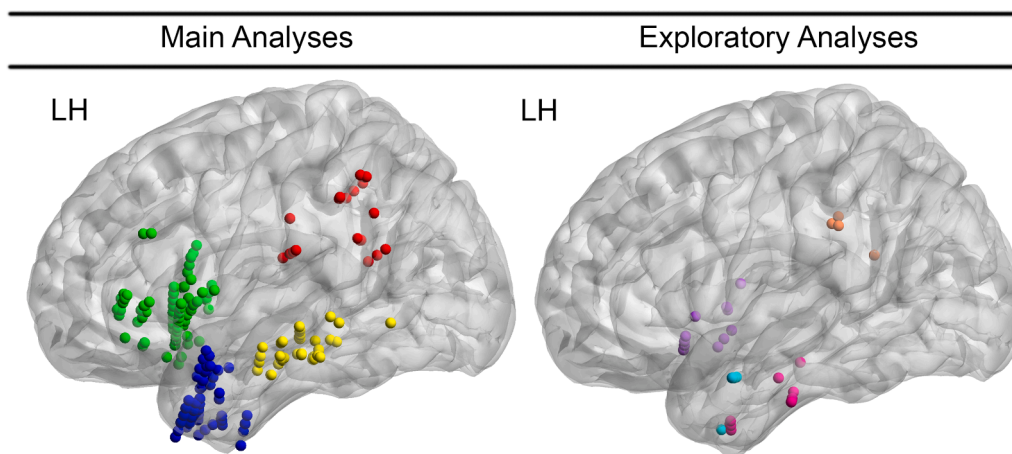
2.6. Exploratory analysis

As noted in the Introduction, a recent connectivity study in post-stroke aphasia (Blackett et al., 2022) found two connections that were specifically related to thematic relations: ITG to insula and MTG pole to PCG. Therefore, in the present study, we further examined phase synchronization for these two connections. These analyses had the same structure as the main analysis above, except the new ROIs were defined as in the Blackett et al. study, based on the Johns Hopkins University neuroanatomical atlas (Faria et al., 2012) (see right side of Fig. 1; MTG-PCC: participant N = 2, electrode pair N = 8; ITG-INS: participant N = 3, electrode pair N = 18).

3. Results

3.1. Behavioral results

There were no significant differences in accuracy ($z = 0.69$, $p = 0.49$) between taxonomic trials (M = 83%; SD = 11%; range = 69%-100%)

Fig. 1. Spatial electrode coverage across participants within the regions of interest. Left: Main analyses, with ATL in blue (n = 56), IPL in red (n = 25), IFG in green (n = 70), and pMTG in yellow (n = 39). Right: Exploratory analysis of connections between posterior cingulate (orange; n = 4) and pole of middle temporal gyrus (brown; n = 4), and inferior temporal gyrus (magenta; n = 8) and insula (purple; n = 11).

and thematic trials (M = 86%; SD = 11%, range = 63%-100%). There were also no significant differences in response time ($t(31.2) = 0.44$, $p = 0.66$) between taxonomic trials (M = 3.84 s, SD = 1.40 s, range = 1.81–6.26 s) and thematic trials (M = 3.62 s, SD = 1.51 s, range = 1.59–6.60 s). The response times were generally slower than normal controls (around 2 s), probably due to the influence of epilepsy, anti-seizure medications, presence of sEEG electrodes, or other aspects of the testing environment. The absence of statistically reliable accuracy or reaction time differences is consistent with previously reported behavioral results from a sample of neurotypical adults (Geller et al., 2019) and further indicates that the control demands were comparable for each condition.

3.2. Theta band (4–7 Hz)

The model estimates for the fixed effects are presented in Table 2. Fig. 2 shows the PLV time course in each ROI pair for taxonomic and thematic conditions. Across all models, the model intercepts within theta band were significantly above zero, but there was no semantic relation type (taxonomic vs. thematic) effect in either of the ROIs. There was a time effect found in IFG-IFG, ATL-pMTG and IPL-IFG, which showed that their overall PLV decreased across time. Critically, a significant interaction effect between time and semantic relation type was found in all connections except ATL-ATL. For the connections of IFG-IFG, pMTG-pMTG, ATL-IFG, ATL-pMTG and IPL-IFG, the PLV on taxonomic trials increased over time relative to the thematic trials, whereas the opposite pattern was observed in IPL-IPL and IPL-pMTG: PLV on thematic trials increased relative to taxonomic trials. These results are broadly consistent with the dual-hub prediction of greater IPL involvement for thematic relations (synchronization within IPL and between IPL and pMTG) and greater ATL involvement for taxonomic relations (synchronization within between ATL and pMTG and IFG), though increased IPL-IFG synchronization on taxonomic trials is not consistent with this account.

The model residuals of the theta band were not normally distributed.

Table 2
The estimates of models for all the ROI pairs in the theta band (4–7 Hz).

ROI Pair	**Fixed effect** Estimate (*SE*), *p* value			
	Intercept	*Time*	*Trial type* [a]	*Time × Trial type*
ATL – ATL	0.04 (0.007), $p < 0.001$**	−0.000 (0.000), $p = 0.19$	0.001(0.008), $p = 0.93$	0.000(0.000), $p = 0.08$
IPL – IPL	0.03 (0.008), $p < 0.001$**	0.000(0.000), $p = 0.29$	−0.001 (0.010), $p = 0.93$	−0.001 (0.000), $p < 0.001$**
IFG – IFG	0.05 (0.004), $p < 0.001$**	−0.000 (0.000), $p = 0.004$**	−0.003 (0.006), $p = 0.55$	0.001(0.000), $p < 0.001$**
pMTG – pMTG	0.05 (0.006), $p < 0.001$**	−0.000 (0.000), $p = 0.56$	−0.005 (0.008), $p = 0.49$	0.001(0.000), $p = 0.01$*
ATL – IFG	0.05 (0.005), $p < 0.001$**	−0.000 (0.000), $p = 0.77$	−0.01 (0.006), $p = 0.09$	0.001 (0.000), $p < 0.001$**
ATL – pMTG	0.05 (0.007), $p < 0.001$**	−0.000 (0.000), $p = 0.001$**	−0.003 (0.010), $p = 0.77$	0.001 (0.000), $p < 0.001$**
IPL – IFG	0.05 (0.007), $p < 0.001$**	−0.000 (0.000), $p < 0.001$**	0.001 (0.008), $p = 0.93$	0.001 (0.000), $p < 0.001$**
IPL – pMTG	0.05 (0.006), $p < 0.001$**	0.000 (0.000), $p = 0.03$*	−0.007 (0.008), $p = 0.37$	−0.001 (0.000), $p = 0.003$**

ATL = Anterior Temporal Lobe; pMTG = posterior Middle Temporal Gyrus; IFG = Inferior Frontal Gyrus; IPL = Inferior Parietal Lobule. [a] 0 = thematic, 1 = taxonomic. *p < 0.05. **p < 0.017 (corrected α).

Therefore, we Box-Cox transformed the PLV data and re-ran the analysis. The new residuals' distribution was acceptable and the result pattern did not change (see SI Table 1). We further examined the impact of RT on PLV by adding RT as a fixed effect covariate and by-participant random slope. The fixed effect of RT was not significant and other results remained the same (SI Table 2). The exploratory analyses of timing revealed two interesting observations. (1) The greater IPL-IFG phase synchronization for taxonomic compared to thematic relations – which is in the opposite direction of the dual-hub account prediction – emerged earliest, within the first 500 ms, when no other effects were statistically significant. (2) Intra-region phase synchronization within ATL, which was weak (marginally significant) in the planned 0–2000 ms window, was stronger in slightly shorter windows (0–1000 ms and 0–1500 ms). (For full results see SI Table 3). The possible implications of these patterns are considered in the Discussion.

3.3. Alpha band (8–12 Hz)

All models had intercepts significantly higher than zero, but no effects of semantic relation type or interactions with semantic relation type were statistically significant in the alpha band models (see SI Table 4 and SI Fig. 1). The model residuals of the alpha band were not normally distributed. Therefore, we Box-Cox transformed the PLV data and re-ran the analysis. The new residuals' distribution was acceptable and the result pattern did not change (see SI Table 5).

3.4. High frequency broadband (70–150 Hz)

The result of HFB is shown in SI Table 6 and SI Fig. 2. The intercept effect in HFB was significantly lower than zero in IPL-pMTG. There was a significant time effect in ATL-ATL, ATL-IFG, and IPL-IFG, with the overall PLV increasing over time. There was a significant interaction between time and semantic relation type only for the ROI pair ATL-IFG ($p < 0.017$): PLVs tended to increase over time more during thematic trials than they did during taxonomic trials. However, as shown in SI Fig. 2, most PLV were negative in HFB, making the results hard to interpret.

3.5. Exploratory analysis

The results of the exploratory analyses are presented in Fig. 3 and SI Table 7. The interactions between time and semantic relation type were marginally significant, though they did not survive multiple-comparison correction. The MTP-PCG ROI pair showed an increasing trend for thematic trials over time relative to taxonomic trials in theta ($p = 0.06$) and HFB bands ($p = 0.04$), though note that the HFB PLVs were consistently negative so they should be interpreted with caution. The ITG-insula pair showed a similar trend of increasing PLV on thematic trials relative to taxonomic trials in the alpha band ($p = 0.03$). These analyses are based on a small number of electrode pairs and the results should be interpreted cautiously, but they are consistent with the pattern reported by Blackett et al. (2022) that these connections are particularly important for processing thematic relations.

4. Discussion

4.1. Summary of results

The present study examined phase synchronization between key semantic processing regions during the processing of taxonomic and thematic semantic relations using sEEG data acquired while participants performed a semantic relatedness judgement task (Thye et al., 2021). The regions of interest were two proposed semantic hubs, the ATL and IPL, and two key semantic control regions, pMTG and IFG. In the theta band (4–7 Hz), synchronization between pMTG and the semantic hubs showed functional specialization consistent with the dual-hub account:
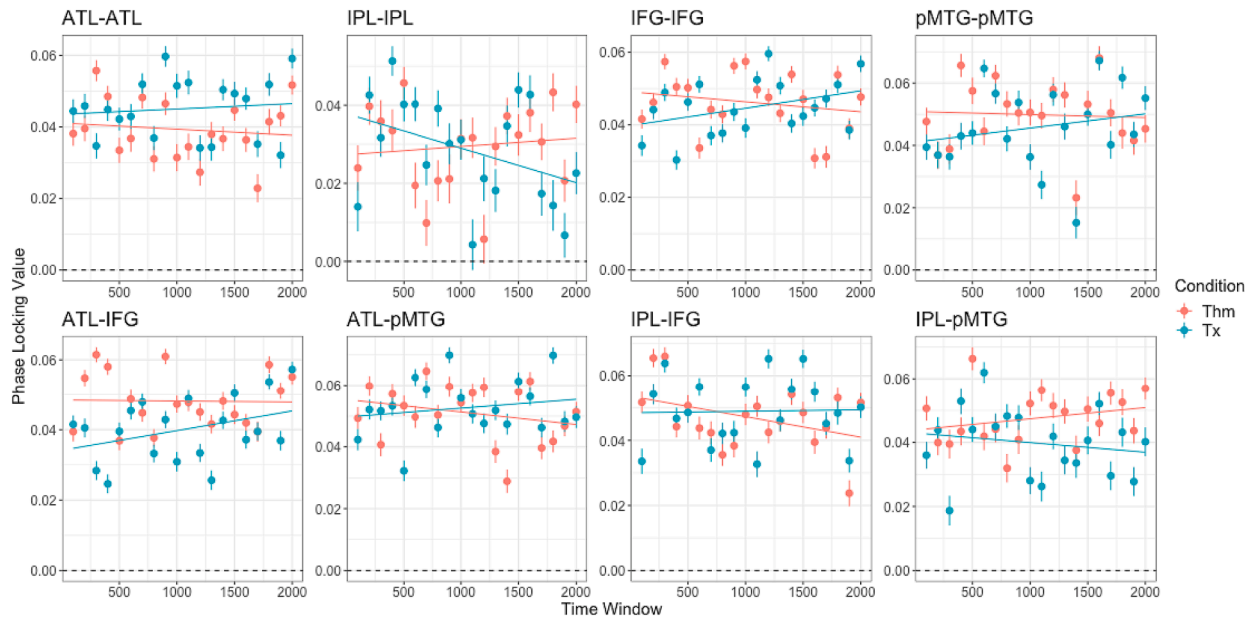
Fig. 2. The averaged PLV and the model prediction for the theta frequency band. Top row shows intra-region phase synchronization, bottom row shows inter-region phase synchronization between semantic hub and semantic control regions. Time (2000 ms after trial onset) is shown on the x-axis and the PLV on the y-axis. Dots with error bars are means and SEs of PLV in each time bin, and the solid lines are model predictions.
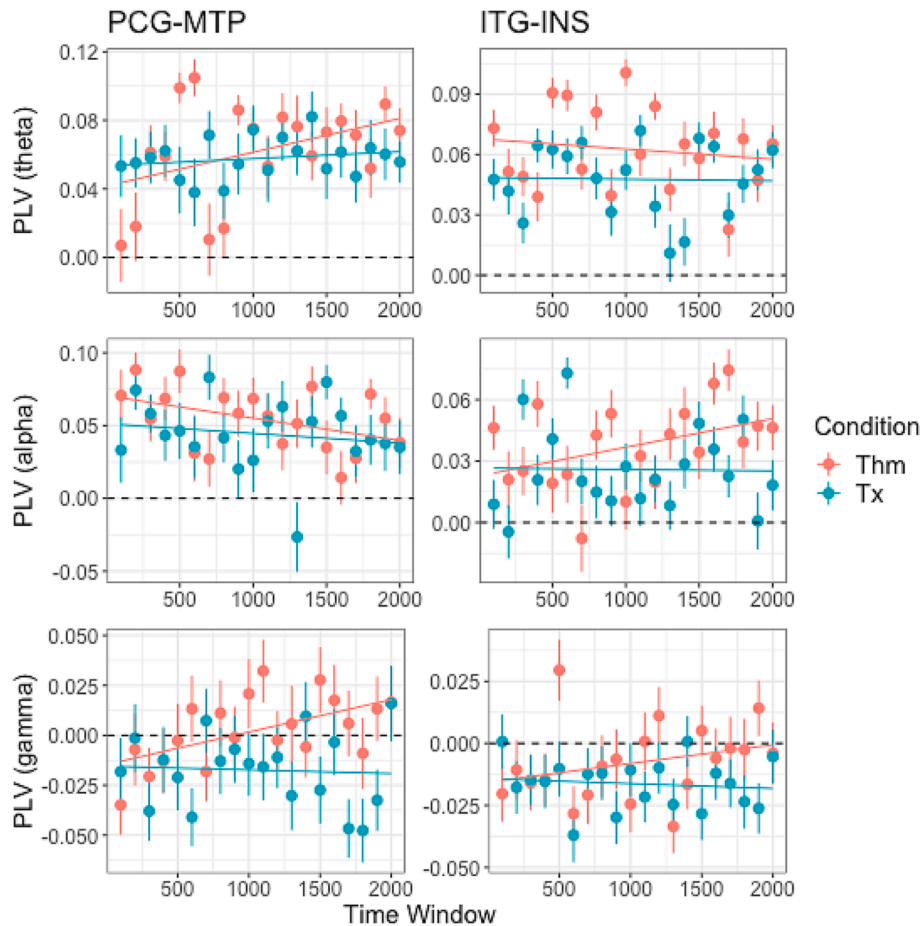
Fig. 3. The averaged PLV and the model prediction for the PCG-MTP and ITG-Insula pairs. Time (2000 ms after trial onset) is shown on the x-axis and the PLVs (phase locking value) on the y-axis. Dots with error bars are means and SEs of PLV in each time bin, and the solid lines are model predictions.

ATL-pMTG synchronization increased on taxonomic trials relative to thematic trials, while IPL-pMTG synchronization increased on thematic trials relative to taxonomic trials. In addition, IPL-IPL synchronization increased during thematic trials relative to taxonomic trials. IFG synchronization with both IPL and ATL increased more on taxonomic trials than on thematic trials (Fig. 4 shows a summary of key effects). The other frequency bands (alpha and HFB) did not show consistent effects of semantic relation type.

4.2. Frequency bands

Results differed across the three frequency bands. Theta band was the most sensitive to neural synchronization during semantic relation processing. This is consistent with our prior analyses (Thye et al., 2021), which showed functional dissociations between taxonomic and thematic processing in lower frequency bands (theta and alpha) and not in the HFB, though the present results are further restricted to the theta band. Theta band synchronization can spread longer distances than high frequency bands, thus helping the communication of distant brain regions, especially between regions of memory representation and executive control (Daume et al., 2017). Even though theta oscillations are not fast enough to induce dense action potentials and encode memory, they help modulate high frequency oscillations by selecting signals with

appropriate timing (Fell & Axmacher, 2011). Scalp EEG studies suggest that theta synchronization underlies neural communication between anterior and posterior regions and supports the retrieval of semantic representations (Mellem et al., 2013). For instance, theta power increases in left temporal regions have been found in response to open-class words but not closed-class words (Bastiaansen et al., 2005). Intracranial and scalp EEG are not directly comparable (e.g., Herweg et al., 2020; Thye et al., 2021), but previous research and the present findings suggest that oscillatory responses and phase synchronization in the theta band are involved in semantic processing and they differ between taxonomic and thematic semantic relations.

It is perhaps surprising that effects were not observed in the alpha or HFB bands. Indeed, in the HFB, PLVs were even lower than baseline or not different from it, suggesting that there was lower or equal phase synchronization during semantic processing compared to baseline. Previous studies have found that HFB power is correlated with BOLD response (Engell et al., 2012; Lachaux et al., 2007), that HFB oscillations support coherent neural processing and memory formation (Bosman et al., 2014; Fell & Axmacher, 2011), and that alpha band synchronization supports coordination in local and large-scale neural networks (Palva & Palva, 2011), and relates to inhibition during working memory (Marzetti et al., 2019). However, it has been suggested that higher frequency (e.g., HFB) synchronization mainly supports short-range neural
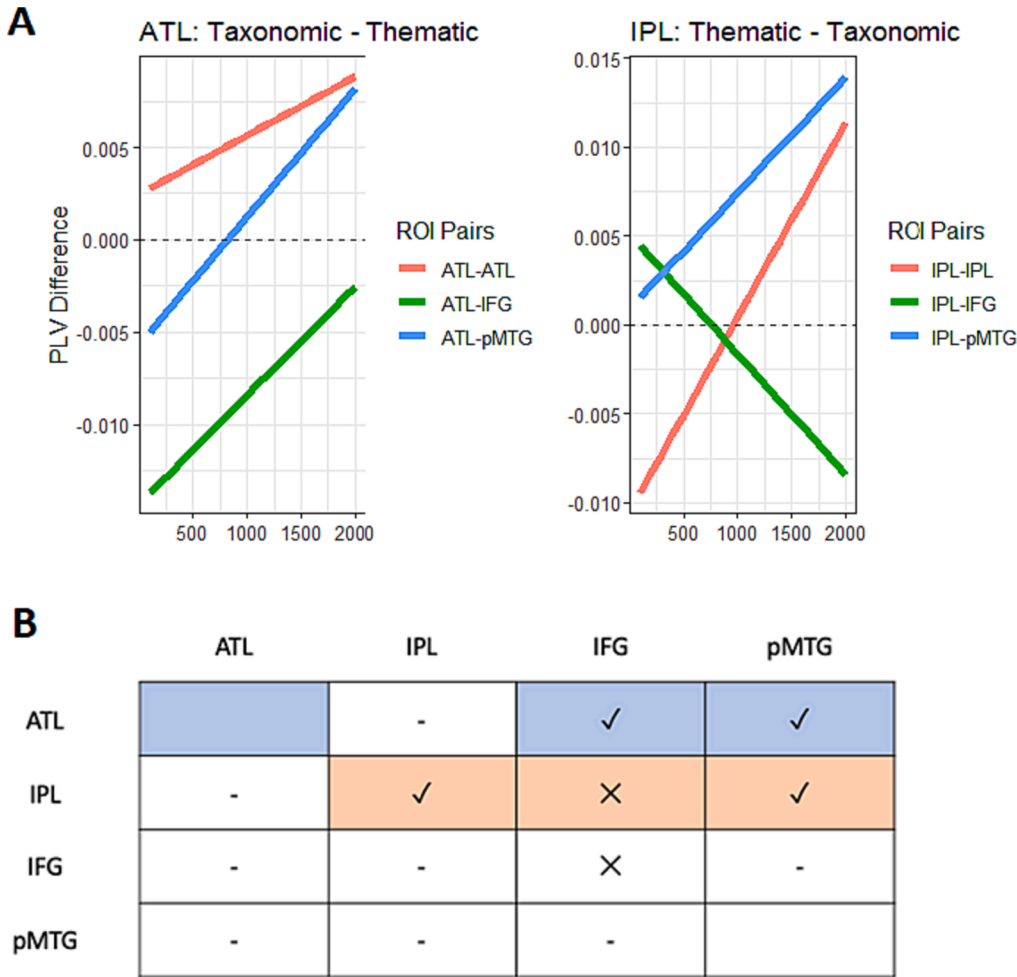
Fig. 4. Summary of predictions and results within the theta band. A. Difference in model predictions between conditions for each region pair of interest. Differences in predicted synchronization within/with the ATL are presented on the left, those in predicted synchronization within/with the IPL are on the right. Time (2000 ms after trial onset) is shown on the x-axis and the difference in predicted PLV between conditions on the y-axis. **B.** The effects predicted by the dual-hub account are indicated with blue shading for Taxonomic > Thematic relations and red shading for Thematic > Taxonomic relations. ✓indicates effects observed congruent with predictions and x indicates effects incongruent with predictions. ATL: anterior temporal lobe; IPL: inferior parietal lobe; IFG: inferior frontal gyrus; pMTG: posterior middle temporal gyrus.

communication, but the key connections studied here were longer-range and phase synchronization within lower frequency bands (e.g., theta) is particularly important for longer-range communication (Canolty & Knight, 2010; von Stein & Sarnthein, 2000).

4.3. Exploratory analysis

Related to the present study's focus on functional connections, a recent connectome-based lesion-symptom mapping in post-stroke aphasia (Blackett et al., 2022) found two structural white-matter connections (ITG-insula and MTP-PCG) involved in thematic relations. Here we further tested whether these structural connections were functionally engaged in thematic relation processing. The available data had only a small number of electrode pairs in those regions, but the evidence suggested that, during thematic trials relative to taxonomic trials, phase synchronization of MTP-PCG was larger in alpha band and HFB and phase synchronization of ITG-insula was larger in the alpha band.

In addition to the effects being weak because of the small number of electrode pairs, the effects for the two connections were found in different frequency bands. As discussed above, signals from different bands might have different functional implications. Thus, although broadly consistent with the Blackett et al. (2022) finding that these connections are particularly important for thematic relations, the function of these connections remains unclear.

Another complication is that the ITG and MTP regions in these analyses are subregions of the ATL region, which showed taxonomic specialization in our previous work (Thye et al., 2021) and which, in the main analyses of the current study, showed greater phase synchronization with semantic control regions (IFG and pMTG) during taxonomic relative to thematic processing. This may reflect functional heterogeneity in the ATL – previous studies have found that sub-regions of the ATL are specialized for different aspects of semantic cognition (Binney et al., 2010; Fan et al., 2014). In addition, the analyses here examined phase synchronization between pairs of regions and it may be that synchronization with semantic control regions has a different functional role than synchronization with PCG, which is part of the default mode network and is involved in autobiographical memory and spatial processing (Leech & Sharp, 2014). Coordination with the PCG may be particularly important for event-based semantic cognition that is engaged for thematic relations.

4.4. The dual-hub account

There is extensive evidence of functional specialization for taxonomic vs thematic relations (reviewed in Mirman et al., 2017) and specifically for the "dual-hub" account that the ATL is specialized for taxonomic relations and IPL for thematic relations. Three recent studies provide particularly compelling evidence using different methods: (1) a registered report using adaptation fMRI (Geng & Schnur, 2016) found ATL specialization for taxonomic relations and IPL specialization for thematic relations; (2) using representational similarity analyses, Xu et al. (2018) found that taxonomic relations had stronger effects in ATL while thematic relations had stronger effects in IPL; (3) the combined sEEG evidence from Thye et al. (2021) and the present study. However, the evidence is not unequivocally consistent. For example, the highly-cited lesion-symptom dissociation reported by Schwartz et al. (2011) was not replicated by Blackett et al. (2022) and the sEEG effects were transient and restricted to only some frequency bands. We propose two general ways to interpret this lack of consistency.

First, small effects should not be detected in every analysis or experiment (Francis, 2012b, 2012a, 2013). Dual-hub specialization effects might be small because (a) the ATL and IPL hubs work together, so the functional specialization is transient, as suggested in Thye et al (2021); (b) the ATL and IPL are large regions and the functional specialization might be in only some sub-regions; indeed, it has been previously demonstrated that ATL has heterogeneous sub-regions (e.g.,

Binney et al., 2010; Lambon Ralph et al., 2017); (c) the location of functionally specialized (sub)regions might vary slightly from person to person, a general issue that has been extensively discussed in motivating the use of functional localizers in fMRI (e.g., (Fedorenko et al., 2010; Frost & Goebel, 2012; Nieto-Castañón & Fedorenko, 2012). Using large anatomical ROIs based on templates and treating them as homogeneous regions is a reasonable starting point, but this may underestimate the degree of functional specialization and contribute to inconsistent results across studies. Future studies could define functionally specialized taxonomic-vs-thematic regions at the individual participant level and test whether that specialization is consistent across different tasks or stimuli.

A second way to interpret the inconsistency of the results is that the taxonomic-thematic distinction may be imperfectly capturing the relevant dimension(s) of functional specialization. We have previously suggested that the taxonomic-thematic distinction may be driven by differences in critical features (i.e., shape and color for taxonomic relations, action and location for thematic relations) or differences between identification/categorization and prediction. Although the feature-type and identification-prediction distinctions broadly align with the taxonomic-thematic distinction, some taxonomic relations rely on action or location features (artefacts in general, and tools in particular) or may have predictive relations in some contexts (e.g., dog and sheep are taxonomically related, but could have a predictive relation in a sheep herding context). As a result, studies that use broad taxonomic-thematic manipulations (such as the present study) may fail to detect a functional specialization effect because they include stimuli that have the opposite underlying property (e.g., taxonomic pairs that rely on action/location features or have a predictive relation). Future studies should directly examine these potential underlying driving forces for functional specialization by using more focused manipulations than the generic taxonomic-thematic distinction (for an example of this approach see Y. Zhang et al., 2023).

4.5. Semantic control

Semantic control refers to the set of executive control processes that regulate the activation and deployment of semantic knowledge, allowing flexible, context- and task-appropriate responses by ensuring that only relevant aspects of semantic representations are used to direct thought and behavior (Jackson, 2021; Jefferies, 2013). There have been some proposals that taxonomic and thematic relations differ in their control demands – some arguing that taxonomic relations require less control (e.g., Thompson et al., 2017) while others argue that thematic relations are easier (e.g., Lawson et al., 2017; Rabovsky et al., 2016; Savic et al., 2017). As a practical matter, it is difficult to answer this question because relatedness strength is the primary determinant of semantic control demands and it is not always clear how to ensure that two very different kinds of semantic relatedness are matched.

For the present study we have independent explicit and implicit, behavioral and psychophysiological evidence that the taxonomic and thematic word pairs were matched in terms of relatedness strength and control demands. First, the stimuli were selected from a prior large-scale norming study (Landrigan & Mirman, 2016), which allows selecting items that have strong taxonomic or thematic relations and, importantly, weak relations of the other type. Second, the stimuli were previously tested in a study with neurotypical adults (Geller et al., 2019), which found no behavioral evidence of differences in difficulty: no differences in response time or accuracy of relatedness judgments. The same lack of behavioral differences between conditions was observed in the present study. It is possible for effective deployment of cognitive control to mask differences in difficulty, so no effects are observed in response time or accuracy data. However, Geller et al. (2019) also found no cognitive effort differences between strongly-related taxonomic and thematic trials based on pupil size, a physiological measure that is sensitive to cognitive effort and control demands (Mathot, 2018; van der

Wel & van Steenbergen, 2018). Therefore, the evidence suggests that relatedness strength and control demands were matched between taxonomic and thematic conditions in this study and differences in control demands do not offer a compelling account of functional specialization of ATL and IPL.

This does leave an unanswered question about why IFG exhibited increased synchronization with itself and with both hubs during the processing of taxonomic relations. It is tempting to propose that taxonomic relations require some additional control processes supported by IFG, but that would contradict the above arguments and evidence that control demands were matched in this study, as well as our prior work that found no additional engagement of IFG for taxonomic relations (Thye et al., 2021). It may be that there is some specific control process involved in taxonomic relations that is supported specifically by theta band synchronization with IFG and is not observable in behavioral or pupil data, but we must leave the identification of such a process to future research.

4.6. Timing of effects

Exploratory analyses were conducted using different time windows to gain additional insights into the timing of the observed differences in phase synchrony for taxonomic and thematic relations. Phase synchronization within ATL was stronger for taxonomic relations than for thematic relations in intermediate time windows: up to 1000 ms and 1500 ms. But this specialization was weaker (marginally significant) in the full 2000 ms time window. These results are consistent with prior work suggesting that semantic responses in ATL emerge quickly after stimulus onset (Lewis et al., 2015; Teige et al., 2019; Thye et al., 2021) and that any functional specialization for taxonomic relations is transient (Thye et al., 2021).

As described above, IPL-IFG phase synchronization was the exact opposite of the dual-hub prediction: it increased more for taxonomic relations than for thematic relations. This pattern emerged very early – within the first 500 ms – and remained consistent for the full 2000 ms time window. It is possible for semantic effects to emerge within 500 ms: the N400 is sensitive to semantic variables and peaks about 400 ms after stimulus onset, and a recent intracranial EEG study found ATL codes semantic representations from 250 ms after picture onset (Y. Chen et al., 2016). However, in the present study, no other effects were statistically reliable within the first 500 ms, nor did our prior analyses of IPL and ATL responses find any effects before 500 ms. Additionally, a recent study found that sensitivity to a semantic variable (concreteness) emerged earlier in ATL than in IPL, and interpreted the IPL effects as indicating a role in the integration between the semantic system and the general memory/cognitive system (Farahibozorg et al., 2022). These various strands suggest that the early-emerging and persistent reversed effect of IPL-IFG phase synchronization may reflect a different aspect of processing than accessing semantic relations, though there is not sufficient evidence to speculate what that might be.

4.7. Limitations

First, the small number of participants and sparse spatial sampling decreased the statistical power. In particular, there was minimal coverage for the exploratory analysis and the posterior MTG. Second, although broadly in the typical range on cognitive tests, the participants were necessarily neurologically atypical and had different epilepsy types, age of seizure onset, and medications, which could influence the results. Third, a recent study has found that the oscillatory part of the signal can be conflated with those of the aperiodic components and provided an improved method for describing the power spectrum of neural signals (Donoghue et al., 2020). That approach is not intended for measuring phase angle, which is the basis of the synchronization measure used in this study, but it would be worth exploring this new method in the future. Finally, the word pairs in this study were specifically

selected to have a strong taxonomic or thematic relation and minimal relation of the other type. More generally, the two relations may coexist and compete, so future studies could use a continuous measure (e.g., rating difference) to study functional specialization for different semantic relations.

5. Conclusions

In conclusion, the present study used sEEG to test neural synchronization during taxonomic and thematic relation processing. A pattern of neural dissociation across ATL and IPL, and their synchronization with pMTG was observed, which is consistent with the "dual-hub account" in which ATL is more specialized for taxonomic relations and IPL is more specialized for thematic relations. These results contribute to the evolving understanding of the roles of semantic hubs and control regions in semantic relation processing.

CRediT authorship contribution statement

Erica Adezati: Conceptualization, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Xianqing Liu:** Conceptualization, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Junhua Ding:** Formal analysis, Validation, Writing – original draft, Writing – review & editing. **Melissa Thye:** Data curation, Formal analysis, Investigation, Writing – review & editing. **Jerzy P. Szaflarski:** Funding acquisition, Investigation, Writing – review & editing. **Daniel Mirman:** Conceptualization, Investigation, Methodology, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Link to data and analysis code is included in the manuscript

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.bandl.2024.105379.

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