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Delineating Region-Specific contributions and connectivity patterns for semantic association and categorization through ROI and Granger causality analysis

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ABSTRACT

The neural mechanisms supporting semantic association and categorization are examined in this study. Semantic association involves linking concepts through shared themes, events, or scenes, while semantic categorization organizes meanings hierarchically based on defining features. Twenty-three adults participated in an fMRI study performing categorization and association judgment tasks. Results showed stronger activation in the inferior frontal gyrus during association and marginally weaker activation in the posterior middle temporal gyrus (pMTG) during categorization. Granger causality analysis revealed bottom-up connectivity from the visual cortex to the hippocampus during semantic association, whereas semantic categorization exhibited strong reciprocal connections between the pMTG and frontal semantic control regions, together with information flow from the visual association area and hippocampus to the pars triangularis. We propose that demands on semantic retrieval, precision of semantic representation, perceptual experiences and world knowledge result in observable differences between these two semantic relations.

1. Introduction

The human ability to comprehend the world relies significantly on the manipulation of an infinite array of concepts through language and their organization into an intelligible structure. These concepts are interconnected based on their similarities, differences, co-occurrences or shared attributes. Semantic processing involves the storage, retrieval and manipulation of meanings and is generally considered a shared process among various semantic relations. However, debates arise concerning how words denoting different conceptual meanings are organized and processed in the brain. As the two commonly examined semantic relations, semantic categorization and semantic association represent two dimensions of the organizational spectrum within the semantic space (Fig. 1). Semantic categorization involves organizing concepts into a vertically extended structure connected by superordinate-subordinate or taxonomic relationships (for instance, coffee and tea are categorized as "beverages"), while semantic association links concepts into a non-hierarchical, web-like conceptual map based on factors such as temporal, physical, spatial or lexical co-occurrence, as well as unifying themes or scenes (Jackson et al., 2015; Sachs et al., 2008). Understanding the neural mechanisms underlying the processing of diverse semantic relations is crucial for elucidating the fundamental principles governing the representation and processing of conceptual information within the human brain. Although research has focused on identifying the brain regions supporting taxonomic and thematic processing, it remains uncertain whether these two types of semantic relations are differentially represented and processed. This study aims to investigate this issue by employing region-specific and

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Fig. 1. A schematic diagram of the associative and hierarchical organization of the mental lexicon. Solid lines between words indicate hierarchical relationships while dotted lines indicate associative relationships. While coffee and tea are associatively related, their categorization as belonging to the broader categories of "beverages" requires tracing their hierarchical membership.

functional connectivity analyses to compare taxonomic and thematic judgments of words.

Semantic categorization entails the hierarchical organization of concepts with superordinate-subordinate relationships, linking concepts based on shared defining features within the same hierarchy level. This category membership information can be seen as a form of declarative or world knowledge that is shared across individuals and cultures, constituting an integral part of semantic representations. Determining the membership of a concept involves retrieving its category label and associated information, similar to tracing a lineage in a pedigree. While members within the same category can have associative relationships (as depicted by the dotted line connecting *coffee* and *tea* in Fig. 1), classifying two concepts under the same category requires retrieving not just their defining features but also a hypernym (e.g., both coffee and tea belong to the category of "beverages"). Mere sharing of perceptual or semantic features (e.g., aroma in the case of coffee and soap) is insufficient for establishing categorical relatedness. This type of linear backtracking process relies not only on embodied and multimodal perceptual features such as color, taste or texture but also on more abstract logical rules and declarative knowledge to assess taxonomic relationships. For example, a banana and an orange are categorized together not due to their appearance, taste or texture, but because both are edible fruits. Commonly cited regions for semantic categorization include the left inferior frontal gyrus (IFG), medial frontal gyrus, MTG, inferior temporal gyrus (ITG) and inferior parietal lobule (Carota et al., 2021; Costanzo et al., 2013; Devlin et al., 2000; Pilgrim et al., 2002; Seghier et al., 2004; Tieleman et al., 2005), and several studies have examined the representation and processing of different category types, such as animate and inanimate (Anderson et al., 2014; Caramazza & Shelton, 1998; Ferreira et al., 2015; Grossman et al., 2002; Pulvermuller et al., 2009; Thompson-Schill et al., 1999). While semantic categorization is often used as a proxy for semantic processing (e.g., Devlin et al., 2000; Pilgrim et al., 2002; Seghier et al., 2011), the process of categorization in lexical semantics extends beyond general processes such as retrieving semantic memory.

In contrast, semantic association involves creating a network that connects concepts based on factors like temporal, physical, spatial or lexical co-occurrence, or common themes or scenes. For example, in a bar scene, words such as "glass," "wine," "barstool," and "nuts" may be associated due to their perceptual or physical co-occurrence, rather than their conceptual similarity or category membership. There is no semantic overlap between the concepts of a glass container and an alcoholic beverage, although a glass is commonly used to contain wine. Associatively related concepts (e.g., glass and wine) may not share common perceptual features, and judging semantic association may require retrieving relevant personal experiences (e.g., having visited a bar) or cultural-specific knowledge (e.g., clay jars are commonly used to contain Chinese rice wine, while glass bottles are used for wine in the west). Integrating semantic information and personal cultural experiences helps create a more comprehensive and accurate representation of semantic associations. Some authors refer to this relationship as a "thematic category" (Sachs et al., 2008).

Extensive research has been conducted on the neural system responsible for representing lexical semantics over the past three decades. It is widely accepted that the left ventrolateral temporal region, temporoparietal junction, inferior parietal lobule, dorsomedial prefrontal cortex, anterior temporal lobe and ventrolateral prefrontal cortex form a core semantic network in the cerebral cortex (e.g., Binder et al., 2009; Hickok & Poeppel, 2004; Price, 2012). This cortical semantic system can be divided into two distinct but interrelated networks: a semantic representation network responsible for encoding, storing and retrieving semantic information, and a semantic control network that provides top-down executive control of semantic information and regulates the retrieval and manipulation of concepts, particularly in tasks involving selection, combination and inhibition (Binder & Desai, 2011; Jackson, 2021; Lambon Ralph et al., 2017).

The representation network comprises the left posterior middle/inferior temporal gyrus (Booth et al., 2002; Hickok & Poeppel, 2004, 2007; Martin, 2007), the angular gyrus (Binder et al., 2009; Chou et al., 2009; Seghier, 2013; Wang et al., 2013), and possibly the fusiform gyrus (BA 37) (Binney et al., 2010; Booth et al., 2002; Pulvermuller et al., 2009), along with the anterior temporal region (Binney et al., 2010; Lambon Ralph et al., 2010; Visser, Embleton, et al., 2010; Visser, Jefferies, et al., 2010). This network can be further divided into modality-specific regions responsible for encoding the embodied representation of concepts and heteromodal hubs responsible for integrating the modality-specific concepts. Perceptual attributes are primarily encoded in modality-specific regions, including the visual, auditory, somatosensory, olfactory, gustatory, motor and emotion cortices. These attributes, together with abstract, amodal information, are integrated at the heteromodal hubs located in the occipitotemporal and temporoparietal convergence zones and the anterior temporal lobe (ATL) to form coherent and integrated conceptual representations. The temporoparietal junction (TPJ), particularly the angular gyrus (AG), a component of the dorsal attention network involved in processing temporal and spatial information, is believed to be crucial for concepts pertaining to time and space (Binder & Desai, 2011; Zhang et al., 2023). On the other hand, the occipitotemporal junction (Binder & Desai, 2011) and the ATL (Binney, Embleton, Jefferies, Parker, & Lambon Ralph, 2010; Lambon Ralph, Jefferies, Patterson, & Rogers, 2017; Lambon Ralph, Sage, Jones, & Mayberry, 2010; Visser, Embleton, Jefferies, Parker, & Lambon Ralph, 2010; Visser, Jefferies, & Lambon Ralph, 2010) are argued to be responsible for representing concrete objects.

The semantic control network is argued to comprise the left inferior frontal gyrus (IFG), specifically the pars triangularis and pars orbitalis (Binder et al., 2009; Hoffman et al., 2015; Lambon Ralph et al., 2017; Wagner et al., 2001) and the TPJ, including the AG and posterior middle temporal gyrus (pMTG) (Jackson, 2021; Noonan et al., 2013). While the involvement of the left IFG in semantic control has been long recognized, debates persist regarding the roles of the AG and pMTG. A recent *meta*-analysis by Jackson (2021) suggests a predominantly left-lateralized cortical network, which includes the IFG, pMTG, posterior inferior temporal gyrus (pITG), and dorsomedial prefrontal cortex, in semantic control. This finding aligns closely with Noonan et al.'s (2013) *meta*-analysis, with the distinction that the AG was associated with semantic representation rather than semantic control in the new analysis. Jackson (2021) posits that sporadic inclusion of the AG in semantic control across studies may stem from domain-general control functions such as inhibition induced by task demands unrelated to semantic functions.

Interestingly, the role of the TPJ, particularly the AG, along with the ATL, in taxonomic and thematic processing is also a topic of ongoing debate. The debate revolves around whether the AG and ATL are exclusively involved in thematic or taxonomic processing, both processes, or neither. Semantic association, which connects concepts based on temporal, physical, spatial or lexical co-occurrence as well as common scenes, integrates conceptual knowledge with personal cultural experiences. The involvement of the AG in thematic processing likely stems from its role in top-down semantic selection and domain-general control functions (Noonan et al., 2013; Thompson et al., 2017). On the other hand, category members share similar perceptual features such as color and shape, and taxonomic processing requires integrating information from different modal-specific brain regions (Lambon Ralph et al., 2017). The ATL serves as a multimodal semantic hub that integrates cross-modal semantic features to form unified concepts (e.g., Lambon Ralph et al., 2010).

Neuroimaging and neuropsychological studies comparing the neural correlates of taxonomic and thematic processing have yielded contrasting findings. The dual-hub hypothesis, which posits that the ATL is the hub for taxonomic relations and the TPJ is the hub for thematic relations, has been supported by neuropsychological studies (e.g., Schwartz et al., 2011) and neuroimaging studies using healthy individuals (e.g., Geng & Schnur, 2016). These studies typically showed that patients with Broca's aphasia were more likely to have difficulties with taxonomic processing, while patients with Wernicke's aphasia were more prone to difficulties with thematic processing (Mirman et al., 2017; Schwartz et al., 2011).

However, many other studies failed to support the dual-hub hypothesis (e.g., Jackson et al., 2015; Lewis et al., 2018; Sachs et al., 2008; Thompson et al., 2017; Zhang et al., 2023). In an early study that compared the representations of these two semantic relations, Sachs et al. (2008) observed priming effects for taxonomically related words in the right precuneus, postcentral gyrus, middle frontal gyrus, and superior frontal gyrus, and for associatively related words in the right anterior middle frontal gyrus and the anterior cingulate. No activation in the AG and ATL was reported. Thompson et al. (2017) discovered that stroke patients with semantic aphasia, who had lesions in the posterior frontal, inferior parietal and/or posterior temporal cortex, exhibited impairments in tasks tapping taxonomic and thematic knowledge. The patients struggled in tasks requiring strong semantic control, especially in thematic conditions with weak associations, indicating that semantic control processes are crucial in assessing thematic associations (see also Chou et al., 2019). In an investigation contrasting thematic and taxonomic processing with or without inhibitory control, Lewis et al. (2019) noted AG activation during thematic processing with or without inhibition of irrelevant semantic content and during taxonomic processing only when inhibition of irrelevant semantic content was required. This finding indicates that the AG is involved in both thematic processing and the inhibition of irrelevant semantic information. However, how the AG is involved in thematic processing and inhibitory semantic processing requires further research for a comprehensive understanding.

In another fMRI study comparing associative pairs with word pairs sharing conceptual properties, Jackson et al. (2015) presented participants with triads of concrete nouns: a probe, a target that was either semantically associated with the probe or conceptually similar to it, and an unrelated foil. Participants were asked to choose between the target and the foil the word that was semantically related to the probe. The study revealed that both types of relationships, associative and conceptual, engaged the same neural network, including the ATL, superior temporal sulcus and ventral prefrontal cortex. After controlling for task difficulty, the authors did not find significant differences between the two processes and concluded that the brain's encodings of semantic features and associations are not distinct.

In their recent *meta*-analysis, Zhang et al. (2023) reported a higher likelihood of activation for processing thematic relations compared to taxonomic relations in the left pMTG and supramarginal gyrus (SMG), and that thematic relations were more reliant on action and location information. There was no evidence that taxonomic relations engaged the left ATL or relied on perceptual features such as color and shape. However, the right lingual gyrus, which processes visual features such as shape and color, was found to show a higher activation likelihood in processing taxonomic relations.

The inconclusive results of previous studies may be attributed to differences in how semantic association and conceptual similarity of word pairs are defined and manipulated. One challenge is finding word pairs that are completely unassociated yet categorically related, leading to varying degrees of overlap between the two semantic relations. Some studies had word pairs with higher overlap in taxonomic and thematic relations (e.g., Kotz et al., 2002; Sachs et al., 2008), while others had less overlap (e.g., Jackson et al., 2015). Consequently, it is challenging to completely eliminate the inherent conceptual overlap between the two types of semantic relations. In addition, these studies generally conceptualized different semantic relations as having different representations, resulting in arguments of different hubs for different types of relations. Accordingly, paradigms that measure automatic or implicit semantic processing and tap into lexical representation, such as semantic priming, were used.

Instead of focusing on the representation differences between taxonomic and thematic semantic relations, this study aims to explore the semantic control processes involved in these two types of semantic relations. We employed functional magnetic resonance imaging (fMRI) and engaged participants in two explicit judgment tasks. In one task, participants judged whether word pairs were semantically associated, while in the other, they judged whether word pairs belonged to the same semantic category. Since the focus was not on representational differences between the two semantic relations, we did not exclude word pairs that shared both categorical and associative relationships. By computing the functional connectivity among the various activated brain regions, we sought to understand the information flow during the processing of these two semantic relations, with a focus on the interaction among areas responsible for encoding perceptual experiences and long-term memory, as well as the regions involved in semantic representation and control.

In sum, we examine how top-down and bottom-up pathways interact and differ during the two semantic relation conditions. To facilitate across-task comparison, we employed a within-subject design. All participants performed semantic association and categorization judgment tasks while being scanned. We predict that the two tasks share a left-lateralized core semantic network, which includes the IFG, pMTG, inferior parietal lobule, and possibly the ATL. The contribution of specific regions and the information flow may vary due to differences in cognitive requirements.

2. Methods

2.1. Participants

Twenty-three native Mandarin speakers were recruited at Peking University (17 males and 6 females; mean age = 21.2 years, SD=1.77 years). They had participated in a previous fMRI study conducted by the authors (Liu et al., 2022). All participants were undergraduate or graduate students, had normal or corrected-to-normal vision, were free of any neurological or psychiatric disorders, and were right-handed as judged by the Edinburgh handedness inventory (Oldfield, 1971) except one participant. The one exception obtained a score of + 40, which is considered marginal between ambidextrous and right-handed. We decided to include this subject in the group analysis, as the activation maps showed a typical left-lateralized pattern. Written informed consent was obtained from each participant, and the study was approved by the Human Research Ethics Committee at the University of Hong Kong. All scanning protocols were approved by the Peking University Institutional Review Boards.

2.2. Materials

Category and association judgment tasks, conducted as two separate runs in the scanner, were used to elicit semantic categorization and association. We selected 28 pairs of Chinese characters that were in the same semantic category (e.g., 斧, 'axe' and 锤, 'hammer') and another 28 pairs that were associatively related (e.g., 云, 'cloud' and 天, 'sky'). An extra 28 pairs of semantically unrelated characters were selected for each task as fillers to balance the number of correct yes and no responses. Ten native Mandarin speakers who did not participate in the fMRI study were asked to rate the categorical relatedness and the associative relatedness of the stimuli used in each task on a scale from 1 to 5. The results of paired t-tests [$t(54) = 61.4, p < 0.001$] confirmed that the experimental stimuli used in the category judgment task were rated higher on categorical relatedness (M=4.58, SD=0.19) compared to the fillers (M=1.35, SD=0.2). Similarly, the experimental stimuli used in the association judgment task were rated higher on associative relatedness (M=4.20, SD=0.34) compared to the fillers (M=1.63, SD=0.36), $t(54) = 27.4, p < 0.001$. The related pairs in the category judgement task were also rated high on associative relatedness (M=4.36, SD=0.21), while those in the association judgement task were rated moderately high on categorical relatedness (M=3.38, SD=0.75). The concreteness and part of speech of the characters are difficult to judge as they are influenced by the context in which the characters appear. However, the related pairs were rated as concrete by the raters (M=4.35, SD=0.85 for the category judgment task and M=3.94, SD=1.13 for the association judgment task). The stroke number which indicates visual complexity and frequency of the characters were matched across the two tasks (Supplementary Table S1).

2.3. Procedures

2.3.1. Stimuli presentation and behavioral data acquisition

The two tasks, category judgment and association judgment, were carried out in separate fMRI runs. The presentation of stimuli and logging of response data were managed using E-prime 2.0. Participants lay in a supine position while viewing stimuli back-projected onto a screen through a mirror mounted in the head coil. In each trial, a pair of characters was simultaneously presented above and below a fixation cross for 2 s, followed by a 500-ms blank screen. The 54 trials, comprising 28 pairs of associatively/categorically related words and 28 pairs of fillers, were grouped into blocks of 14 trials. Each block contained 7 related word pairs and 7 fillers, which were presented in the same pseudorandomized order for all participants. The experimental blocks alternated with font-size judgment blocks in which the participants determined if the two characters had the same size. As cued by the instructions presented for 2 s before each block, participants were explicitly instructed to perform a taxonomical judgment (i.e., judging whether the two characters share a common hypernym) in the category judgment task and to perform a thematic judgment (i.e., judging whether the two characters commonly co-occur) in the association judgment task. Participants indicated a 'yes' response by pressing a button with their right index finger and a 'no' response with their right middle finger. The category and association judgment tasks were parts of a seven-scan fMRI experiment in which participants performed three extra tasks related to Chinese character reading and two tasks related to working memory that are not reported here. The order of performing the five Chinese reading tasks was counterbalanced among the participants. Participants were familiarized with all the tasks using materials that did not overlap with the experimental stimuli before the scans.

2.3.2. Image acquisition

Functional magnetic resonance imaging (fMRI) data were acquired with a 3 T Siemens Magnetom Prisma scanner in the Centre for MRI Research at Peking University. High-resolution ($0.5 \times 0.5 \times 1$ mm^3) T1-weighted anatomical brain images were acquired using a three-dimensional magnetization-prepared rapid acquisition gradient-echo sequence [repetition time (TR) = 2530 ms, echo time (TE) = 2.98 ms, inversion time = 1100 ms, flip angle (FA) = 7°, number of slices = 192], while fMRI data were collected using a T2*-weighted gradient echo-planar imaging sequence (TR=2000 ms, TE=30 ms, FA=90°, number of slices = 33, interleaved, slice thickness = 3.5 mm, gap = 0.7 mm, matrix = 64×64, in-plane resolution = 3.5×3.5 mm^2). Each scan contained 155 volumes and lasted for 310 s.

2.4. Data analysis

2.4.1. Preprocessing

Image preprocessing and statistical analyses of fMRI data were performed in MATLAB 2019b and SPM12. The default preprocessing pipeline in the CONN toolbox (Whitfield-Gabrieli & Nieto-Castanon, 2012) was adopted. Functional images were first time-sliced and motion-corrected. Outlier scans were then identified by the ART-based outlier detection procedure, where images with framewise displacement greater than 0.9 mm or with global BOLD signal changes greater than 5 SDs were identified for scrubbing (Nieto-Castanon, 2020). In total, 16 scans from 4 participants were identified as motion- or signal-change outliers; the maximum number of scans discarded within the same run was 5. The functional images were then segmented and normalized to the ICBM standard template in MNI space at a resolution of $2 \times 2 \times 2$ mm, and smoothed with an isotropic 8-mm full-width at half-maximum Gaussian kernel.

2.4.2. First and second level analysis

Preprocessed images of individual participants were submitted to a first-level analysis using a general linear model. The experimental task and baseline blocks were modeled by two separate regressors that were convolved with a canonical hemodynamic response function. The six head motion parameters estimated during the motion correction step, independent regressors for the scrubbed scans and the global BOLD signal change were included to regress motion artifacts and to remove the effects of motion and signal change spikes, respectively. The time series data were highpass filtered at 128 s and modeled by FAST (Corbin et al., 2018). Group activation t-maps for each task were then obtained by performing second-level random-effect analysis on the contrast images between the task and baseline blocks for each participant. To reveal the activation differences between the semantic association and categorization tasks, the t-contrast maps obtained from the two tasks were entered into a paired sample t-test with subject as the blocking factor. To further determine the common network for the two tasks, a conjunction analysis at the second level was conducted. The activation of the association and categorization tasks were tested against the conjunction null (Nichols et al., 2005). An uncorrected p-value of 0.001 and a familywise error rate (FWE)-corrected p-value of 0.05 were applied to the voxelwise and cluster-level statistical significance analyses for all contrasts.

2.4.3. ROI analysis

To further compare the relative contributions of each region in the semantic network to the two tasks, a region-of-interest (ROI) analysis was conducted. To avoid circularity of the ROI analysis and Granger causality analysis (next section) from the whole brain analysis and to choose ROIs that reflect the generic semantic network, we used a separate semantic task from the same batch of participants. Specifically, the ROIs were defined from a synonym judgment task performed by the same participants in a study previously published by the authors (Liu et al., 2022). The synonym judgement task shares the same format as the association and categorization tasks, with participants asked to judge if the two characters simultaneously presented have the same meaning. The synonym judgment task entails retrieval and comparison of word meanings and is considered to activate the basic semantic representation network. We conducted a second-level analysis of the data of the current batch of participants using the same threshold as described in the previous paragraph. The activation pattern is shown in Supplementary Figure 1. The activation map was converted into a 2 × 2 × 2 mm binary mask and each ROI was created by intersecting the mask with a Brodmann area map (Lacadie et al., 2008). ROIs containing fewer than 20 voxels were excluded. In total, 16 ROIs from the left hemisphere and 6 ROIs from the right hemisphere were generated. The average contrast estimates of the two tasks were then extracted from the respective ROIs for each participant. Repeated-measures ANOVA was performed on the contrast estimates of each ROI with Task as the within-subject factor using the lme4 package in R (Bates et al., 2015). Post-hoc pairwise comparisons between the two tasks were performed with the emmeans package (formerly the lsmeans package; Lenth, 2016). To account for multiple comparisons involving the 22 ROIs and the post hoc tests, a Bonferroni-corrected *p*-value of 0.05 was applied.

2.4.4. Granger causality analysis

To examine the directed information flow within the semantic network during Chinese reading, a Granger causality (GC) analysis was conducted. The principal eigenvariates of the preprocessed fMRI time series were extracted from the previously defined ROIs for each participant. To specifically test whether the difference between semantic categorization and association activation lies in differences in semantic control and the involvement of perceptual experiences or long-term memory, we specifically chose ROIs from the following regions: 1) left IFG (par triangularis and pars orbitalis), 2) left pMTG, 3) left visual cortex (visual association area and the extrastriate cortex) and 4) left hippocampus. As no significant activation was observed in the AG and ATL, these two regions were not selected as ROIs in this study. The values of the GC between the 6 ROIs in these regions were calculated with the MVGC toolbox in MATLAB (Barnett & Seth, 2014). The order of the autoregressive model was determined by the Akaike information criterion. F statistics were used to determine the statistical significance of the GC values at a threshold of $p < 0.05$ with Bonferroni correction.

3. Results

3.1. Behavioral results

The accuracy rates and reaction times for the two tasks are reported in Supplementary Table S2. A 2 × 2 Task (association vs. categorization) by Block-Type (experimental blocks, i.e., association / categorization vs. baseline) factorial ANOVA was performed on the accuracy rates and reaction time in R. The main effects and interaction effect with the accuracy data were not significant [Task: $F(1,90) = 0.0936$, $p = 0.7603$; Block Type: $F(1,90) = 0.0566$, $p = 0.8123$; interaction: $F(1,90) = 0.0012$, $p = 0.9730$], meaning that participants performed equally well in the association blocks, categorization blocks and the font-size blocks. When examining the reaction times, a significant main effect of Block Type was found ($F(1,90) = 41.9$, $p = 5.304 \times 10^{-9}$), showing that the reaction times in the baseline blocks were shorter than those in the semantic relation task blocks. The main effect of Task and the interaction term were not significant [Task: $F(1,90) = 1.1914$, $p = 0.278$; interaction: $F(1,90) = 1.5276$, $p = 0.2198$]. The absence of a main effect of Task and Task-by-Block-Type interaction indicated that the two semantic tasks were equally demanding compared to their respective baseline tasks, justifying across-scan comparisons.

3.2. Whole-brain analysis reveals a common fronto-parieto-temporal semantic network

Due to the gender imbalance, we first examined if there were any activation differences due to gender. An independent-sample *t*-test comparing males and females was conducted. No clusters survived any task contrast comparisons (voxel-level: $p = 0.001$, uncorrected; cluster-level: $p = 0.05$, FWE corrected). The fMRI data for all participants were thus pooled together for subsequent analyses.

Activation patterns and peak coordinates in individual tasks are reported in Fig. 2 and Supplementary Table S3. Both tasks commonly activated a large region in the left dorsal and ventral lateral prefrontal cortices, including the middle frontal gyrus (MFG, BA 9/46), pars opercularis (BA 44), pars triangularis (BA 45), pars orbitalis (BA 47), bilateral medial frontal gyrus (MeFG, BA 6/8), left superior parietal lobule (SPL, BA 7), left fusiform gyrus (FFG, BA 37), left posterior middle temporal gyrus (pMTG, BA 21), left visual association area (BA 18) and the right cerebellum. The association task additionally recruited the bilateral insula (BA 13), the right lateral prefrontal cortex (IFG: BA 44 and 45; MFG: BA 9 and 10) and the right caudate.

The results of the paired *t*-test revealed significantly stronger activation in the left inferior frontal gyrus (BA 44), precentral gyrus (BA 6), inferior temporal gyrus (BA 37) and middle temporal gyrus (BA 21) during the semantic association task. No clusters survived multiple comparisons for the categorization > association contrast.

Results of the conjunction analysis are reported in Fig. 3 and Supplementary Table S4. Consistent with the task-specific contrasts, commonly activated regions across the two tasks include the left MFG (BA 46), pars opercularis (BA 44), pars orbitalis (BA 47), left MeFG (BA 6/8), left SPL (BA 7) and right pars triangularis (BA 45). However, some regions that are activated in the two individual contrasts do not survive the conjunction analysis, including the left pMTG (BA 21), left FFG (BA 37), left visual association area (BA 18) and the right cerebellum.

3.3. ROI analysis reveals stronger activation during semantic association judgment

The contrast estimates of the ROIs from each task are plotted in Fig. 4, with the statistics reported in Table 1. In general, semantic association exhibited stronger activation at all the ROIs. Following Bonferroni correction for multiple comparisons, significant differences were found in the left par opercularis (BA 44), par triangularis (BA 45) and pars orbitalis (BA 47). Marginally significant differences were found at the left medial frontal gyrus (BA 8), left pMTG (BA 21) and the right pars triangularis (BA 45).

3.4. Brain connectivity differences between the two semantic networks

The GC values of the association and categorization tasks are reported in Table 2. The order of the model for both tasks was set to 1. We focus on the significant connections between functionally delineated regions below.

During semantic association, significant effective connectivity was observed from the extrastriate cortex to the hippocampus (BA19 to BA 54). The pMTG (BA 21) showed significant connections to the extrastriate cortex (BA 19), pars orbitalis (BA 47) and hippocampus (BA 54). There was also a significant connection from the pars triangularis (BA 45) to the pMTG (BA 21).

During semantic categorization, there was significant bottom-up connectivity from the visual association area (BA 18) to the pars triangularis (BA 45). The pMTG showed significant connections to the extrastriate cortex (BA 19), inferior frontal semantic regions (BA 45, 47) and the hippocampus (BA 54), while significant reciprocal connectivity was seen from the pars triangularis (BA 45) back to the pMTG. Finally, the hippocampus acted as an information source for the pars triangularis.

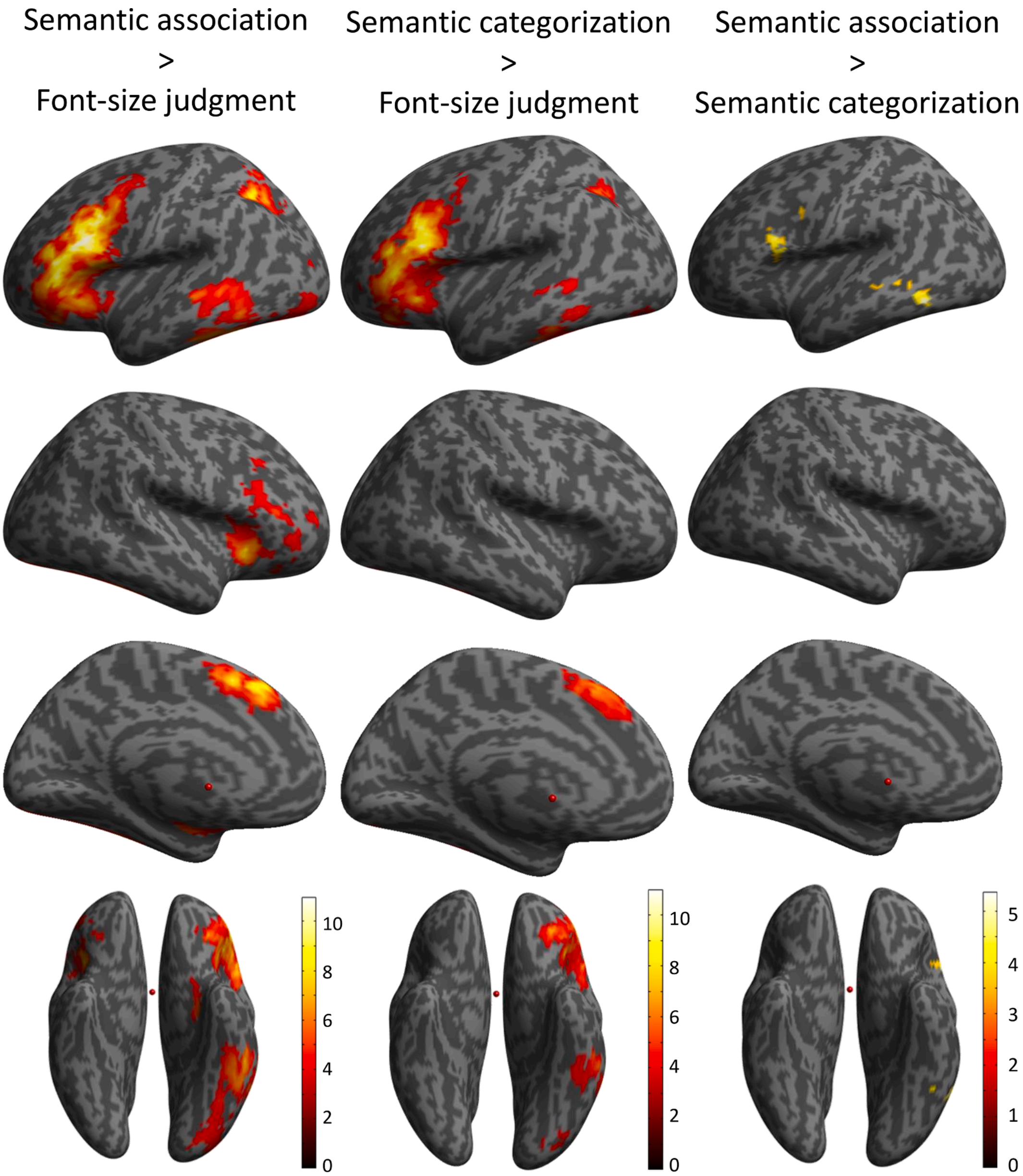

Fig. 2. Activation maps of the fMRI contrasts rendered on an inflated brain surface. Colorbars indicate t-values.

4. Discussion

This study compares the neural networks of two subtypes of lexical semantic processing: semantic association and semantic categorization. It is hypothesized that these two processes share a common semantic network that underlies the basic process of retrieving semantic representations from the visual word form. Considering the distinct demands on semantic representation and control in each task, the explicit process of performing the two tasks may elicit different activation levels at specific functional sites and exhibit different connectivity patterns. This study employed whole-brain analysis, ROI analysis and Granger causality analysis to probe into the overall semantic network, region-specific contributions to each task, and information flow within each network, respectively.

4.1. The core semantic network for Chinese character reading

Regions commonly activated across the two semantic judgement tasks include the left middle and inferior frontal gyrus (especially the pars triangularis and orbitalis), fusiform gyrus, superior parietal lobule/intraparietal sulcus, right inferior frontal gyrus/insula, cerebellum and bilateral medial frontal gyri. The conjunction analysis confirms the involvement of the left middle and inferior frontal gyrus, superior parietal lobule and the right inferior frontal gyrus in the core semantic network. Apart from the absence of the left pMTG and AG and the presence of the left superior parietal lobule, these regions align with most *meta*-analyses on semantic processing (e.g., Binder et al., 2009; Rodd et al., 2015; Wu et al., 2012) and a recent *meta*-analysis on semantic control (Jackson, 2021). Both tasks entailed retrieving meaning from visual stimuli, followed by making a semantic decision on the meaning of the two characters. This process involves recognizing the visual forms, accessing the orthographic lexicon and mapping entities to corresponding semantic representations (Perfetti & Tan, 1999; Perfetti et al., 2005; Perfetti & Tan, 1998). As the contrasts were obtained from the comparison to font-size judgment, activation related to orthographic processing, including the left mid fusiform gyrus (also known as the visual word form area, VWFA, Cohen et al., 2000), superior parietal lobule and possibly the middle frontal gyrus, should have been reduced

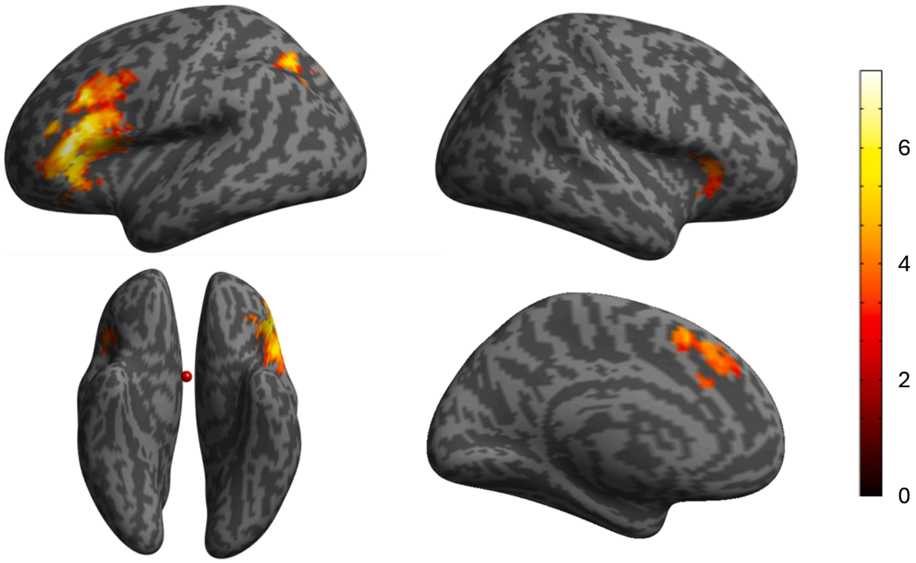

Fig. 3. Results of conjunction analysis on the semantic association and categorization task rendered on an inflated brain surface. Colorbars indicate t-values.

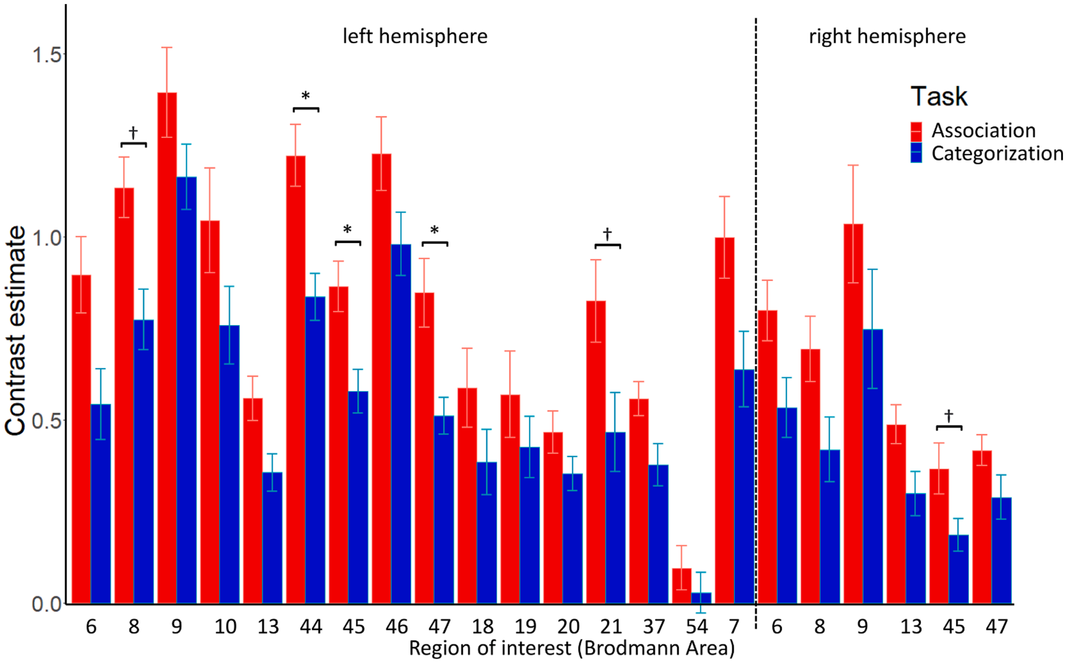

Fig. 4. Contrast estimates of semantic tasks > font-size judgement over 22 ROIs and statistical significance of the paired t-tests. †: p < 0.1. *: p < 0.05. **: p < 0.005.

if not completely eliminated. Notwithstanding, the activations of these regions were still prominent, likely due to the extra cognitive effort involved in visuo-orthographic processing of the finer stroke patterns that font-size judgment does not require (Liu et al., 2022). It should be noted that the left pMTG did not survive correction for multiple comparisons in the conjunction analysis and will be discussed in terms of the activation differences across the two tasks in the results of the ROI analysis.

Two commonly reported regions for semantic processing, the angular gyrus (AG) and the anterior temporal lobe (ATL), were not found in our study. Some of the relevant functions of the AG include semantic processing, word reading and comprehension, memory retrieval, attention and temporal and spatial processing (for a review, see Seghier, 2013). It also plays a crucial role in alphabetic reading (Hoeft et al., 2006; Shaywitz et al., 1998; Temple et al., 2001), phoneme discrimination (Turkeltaub & Coslett, 2010) and phonological awareness tasks (Turkeltaub et al., 2003). In a study of semantic association with a parametric design on association strength, stronger activation was observed in the AG for Chinese characters with stronger semantic association (Chou et al., 2009). A possible explanation for its absence in our study is that the AG is part of the default-mode network (Damoiseaux et al., 2006; Michael et al., 2002; Raichle, 2015). Compared to the easier baseline task on font-size judgment (as indicated by shorter reaction time), the semantic tasks may have recruited more attention and led to greater suppression of the default mode network. Another possibility is that our semantic stimuli did not require the integration of heteromodal features or the inhibition of irrelevant information, functions that are proposed for the angular gyrus (Jackson, 2021; Seghier, 2013).

The left ATL lobe has been implicated in various cognitive processing including sentence processing (Hickok & Poeppel, 2007), grammatical processing (Hickok & Poeppel, 2004), heteromodal integration of

Table 1

Statistics for the within-subject t-tests on the contrast estimates of association > categorization over 22 ROIs. All p values have been Bonferroni corrected. †: $p < 0.1$. *: $p < 0.05$. BA: Brodmann area.

		Regions	BA	MNI coordinates of centroid			*t*	*p*
				x	y	z		
Left	Occipital lobe	visual association cortex	18	−30	−88	−8	1.51	1
		extrastriate cortex	19	−35	−80	−11	1.14	1
	Temporal lobe	posterior inferior temporal gyrus	20	−49	−37	−24	2.10	1
		posterior middle temporal gyrus	21	−56	−39	−4	3.24	$0.0824^{\dagger}$
		fusiform gyrus	37	−47	−45	−20	2.73	0.2704
		hippocampus	54	−31	−12	−21	2.31	0.6674
	Parietal lobe	superior parietal lobule	7	−27	−58	39	2.49	0.4592
	Frontal lobe	pars opercularis	44	−46	15	21	3.93	0.0156*
		pars triangularis	45	−46	26	6	3.63	0.0326*
		pars orbitalis	47	−42	30	−9	3.66	0.0301*
		middle frontal gyrus	46	−46	35	12	2.23	0.7981
			9	−45	24	29	1.88	1
			10	−41	43	−4	2.45	0.4951
		superior frontal gyrus	8	−27	18	41	3.16	$0.0994^{\dagger}$
		precentral gyrus	6	−38	4	45	2.84	0.2075
		anterior insula	13	−33	21	−1	2.64	0.3269
Right	Frontal lobe	pars triangularis	45	32	28	5	3.18	$0.0957^{\dagger}$
		pars orbitalis	47	33	30	−6	1.92	1
		middle frontal gyrus	9	52	26	30	1.47	1
		precentral gyrus	6	4	13	55	1.95	1
		medial frontal gyrus	8	4	25	46	2.31	0.6732
		anterior insula	13	31	24	−2	2.50	0.4510

Table 2

Granger causality values between each pair of nodes. *: $p < 0.05$; **: $p < 0.005$; ***: $p < 0.0005$, Bonferroni corrected.

Granger causality ($\times 10^{-4}$)							
Semantic association							
		from					
		BA18	BA19	BA21	BA45	BA47	BA54
to	BA18		184.22***	1.684	0.997	0.207	11.484
	BA19		54.437***	56.109***	0.15	5.746	18.572
	BA21	24.898	1.671		172.646***	0.016	23.354
	BA45	26.623	0.004	6.863		102.926***	2.777
	BA47	10.269	0.003	37.371**	16.652		6.969
	BA54	26.577	49.204***	110.274***	0.005	5.805	
Semantic categorization							
		BA18	BA19	BA21	BA45	BA47	BA54
to	BA18		142.955***	3.759	0.341	0.083	12.561
	BA19	30.497*		71.717***	5.847	0.002	14.15
	BA21	21.003	0.557		174.222***	0.317	1.297
	BA45	36.721*	7.45	30.538*		4.074	48.654***
	BA47	9.811	1.043	58.686***	12.897		9.408
	BA54	0.737	1.685	97.176***	8.428	14.092	

meaning important for taxonomic processing (Jackson, Hoffman, Pobric, & Lambon Ralph, 2015; Lambon Ralph, Jefferies, Patterson, & Rogers, 2017; Visser, Embleton, Jefferies, Parker, & Lambon Ralph, 2010) and combinatorial semantic processing important for sentence comprehension (Hickok & Poeppel, 2007). It should also be noted that as the ATL is close to air-filled sinuses, it is frequently susceptible to signal loss (Devlin et al., 2000; Halai, Welbourne, Embleton, & Parkes, 2014; Visser, Embleton, Jefferies, Parker, & Lambon Ralph, 2010) and the absence of its activation does not necessarily indicate that the ATL is not involved in semantic processing. To address this concern, we calculated and compared the temporal signal-to-noise ratio (tSNR) of the left ATL with other ROIs and the whole brain. Although the tSNR in the ATL is lower than the whole brain average and most ROIs, it falls within an acceptable range for fMRI studies. As a result, we consider the tSNR in the left ATL for this study to be acceptable and unlikely to be the cause of the absence of significant activation in this region. Therefore, the absence of ATL activation in our findings is like due to the nature of our tasks – not requiring strong combinatorial processing of meaning – rather than our scanning parameters not being optimized to capture signals from this specific region (see Qin et al., 2021 for a similar argument).

4.2. Differential contributions of specific regions in the semantic network

The ROI analysis revealed significantly stronger activation at the left pars opercularis, pars orbitalis and the pars triangularis and marginally significantly stronger activation at the pMTG (note it was in one of the two clusters which survived cluster-level correction in the whole brain association > categorization contrast) when participants were performing the semantic association task. It is well documented that the ventral lateral inferior frontal regions are part of the semantic control network (Binder & Desai, 2011; Binder et al., 2009; Lambon Ralph et al., 2017). In particular, these regions control access to semantic representations, resolve lexical ambiguities, and are engaged when selection demand on the semantic content is high (e.g., Bookheimer, 2002; Bunge et al., 2005; Thompson-Schill et al., 1997; Wagner et al., 2001). Some researchers further propose a specialization in the functions of the pars triangularis and pars orbitalis, attributing a postretrieval selection role to the former and a controlled access role to the latter (Badre & Wagner, 2007). The current results indicate that semantic association required both more effortful semantic retrieval and selection, possibly due to the lack of a direct lexical meaning relationship between the two characters. Given the task nature of the current study, the participants had to perform overt semantic analysis on the character pairs, and the analytic processes of the association relationship can require more effort than the other two types of semantic relationships. To judge whether the two characters are thematically related, the meaning of the two characters must be completely accessed before the relevant senses of the characters are subsequently compared and selected. To illustrate, 线 means ‘thread’, ‘line’ or ‘route’, while 针 means ‘needle’, ‘pin’, ‘sting’ or ‘injection’. Participants had to select the sense ‘thread’ and ‘needle’ based on their frequent co-occurrence or experience in using them, but not the lexical meaning of these characters. In contrast, characters in semantic categorization are related by a hypernym. Upon seeing one of the characters, it would be easier to retrieve the meaning of another, and this may be analogous to the priming effect (Sachs et al., 2008). This may lead to weaker activation in the inferior frontal control regions during semantic categorization.

Previous reviews attribute the roles of the left pMTG to the sound-meaning interface (Hickok & Poeppel, 2004), storing perceptual information about objects and their attributes (Binder & Desai, 2011; Binder et al., 2009), and semantic control (Lambon Ralph et al., 2017). These functions point to its importance in retrieving semantic representations. Our results show that when performing semantic association judgment tasks, there is a trend that these processes were more strongly recruited, but not during the semantic categorization task. Our interpretation is that performing the semantic analysis of associative pairs requires stronger semantic representations of the characters relative to performing the categorical analysis. On the one hand, as the two characters during semantic association are thematically related or the concepts co-occur temporally or spatially, it is necessary to activate relevant experiences or perceptions of the concepts before the two characters can be associated. This results in a stronger degree of embodiment of the concepts (Binder & Desai, 2011). In contrast, semantic categorization may engage less in the perceptual encoding of the concepts as in semantic association. Instead, it requires access to the hypernym of the target items or the world knowledge that the two concepts are taxonomically related. As a result, the activation level in the pMTG during semantic categorization was lower than that during the other two tasks.

Although we have not formally tested the overall activation levels of the right prefrontal cortex, it is noted that semantic association recruited this area to a much larger extent (see Fig. 2 and ROI analysis). It has been suggested that the right prefrontal cortex is involved in the retrieval of episodic memory (Fletcher et al., 1998; Henson et al., 1999; Lepage et al., 2000). This is consistent with the hypothesis that relevant experiences or perceptions are activated when processing the thematic association between two characters.

4.3. *Differences in effective connectivity patterns*

While we have not attempted a formal comparison between the Granger causality values of the two tasks, we found different patterns in effective connectivity. Specifically, during semantic association, information is passed from the visual cortex to the hippocampus, while visual information is passed to the pars triangularis during semantic categorization. While both semantic processes involve information output from the pMTG to the pars orbitalis and hippocampus, there is an additional connection from the pMTG and hippocampus to the pars triangularis during semantic categorization.

The information flow from the visual association area to the hippocampus during semantic association supports our hypothesis that the process relies more on the perceptual encoding of the concepts in context. In fact, during semantic association, the hippocampus receives information from the visual association cortex and the left pMTG. Given the role of the pMTG in semantic representation, the two connections could be interpreted as the combination of abstract conceptual encoding and visual perceptual encoding in the episodic memory center. The successful combination, i.e., the retrieval of contextual meaning, is crucial for semantic association.

Another key difference between the two networks is that semantic categorization demonstrated more extensive coupling between the left temporal semantic center, pMTG and the two frontal semantic regions. It has been discussed that semantic categorization requires the application of world knowledge about the hypernym of the taxonomic relationship of the two characters. As this knowledge is not retrieved from the lexical meaning of the characters, it is less salient than associative relationships. We hypothesize that the connection between the semantic centers on the temporal and frontal lobe is responsible for searching for this abstract relationship through the hierarchical organization of lexical meaning. It is possible that the representation of the less salient hierarchical relationship during semantic categorization is encoded in neural computations that spans the two semantic regions and is manifested in terms of functional connectivity between them.

Interestingly, we found significant connections from the visual association area and the hippocampus to the pars triangularis during semantic categorization but not association. Given the findings of Zhang et al. (2023) about the activation in the right lingual gyrus during taxonomic processing and their proposal concerning the involvement of shape and color processing, we do not exclude the possibility that visual information is passed directly to the frontal semantic control region. In fact, most taxonomic pairs used in our experiment are concrete, and it is likely that participant might have utilized visual imagery to aid judgement. In contrast, the connection from the hippocampus to the pars triangularis may reflect the use of world knowledge about hypernyms (which our task demanded) stored in the long-term memory system.

5. Conclusion

In summary, this study has revealed distinct neurocognitive mechanisms underlying semantic association and semantic categorization in overt semantic analysis tasks. Despite both processes falling under the umbrella of semantic processing, they differ in their requirements for semantic retrieval, representation, meaning selection, world knowledge and perceptual experience. These differences are reflected in the recruitment of specific brain regions, varying activation strengths at semantic-specific sites, and patterns of brain connectivity. Specifically, semantic association involves linking lexical meaning to perceptual experiences, leading to more embodied semantic representations. On the other hand, semantic categorization entails integrating word meaning with nonlexical world knowledge, particularly hierarchical or taxonomic relationships. Our findings support the understanding that different brain regions function dynamically, coherently and collaboratively, highlighting the necessity to shift research focus from a static, representation-based perspective of neural processing to a more dynamic and process-based viewpoint. This work provides valuable insights for future investigations in the field of semantic processing, emphasizing the significance of making nuanced distinctions between the two types of semantic relations.

CRediT authorship contribution statement

Chun Yin Liu: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Lang Qin:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Ran Tao:** Writing – review & editing, Methodology, Investigation, Conceptualization.

Wenxiyuan Deng: Writing – review & editing, Methodology, Investigation. **Tian Jiang:** Writing – review & editing, Methodology, Investigation. **Nizhuan Wang:** Conceptualization, Formal analysis. **Stephen Matthews:** Writing – review & editing, Supervision, Conceptualization. **Wai Ting Siok:** Writing – review & editing, Writing – original draft, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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

Data will be made available on request.

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Data and code availability.

The data and code used in this study are available upon request to the authors through a formal data sharing agreement.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.bandl.2024.105476.

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