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Doctor, Teacher, and Stethoscope: Neural Representation of Different Types of Semantic Relations

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Abstract

Concepts can be related in many ways. They can belong to the same taxonomic category (e.g., “doctor” and “teacher,” both in the category of people) or be associated with the same event context (e.g., “doctor” and “stethoscope,” both associated with medical scenarios). How are these two major types of semantic relations coded in the brain? We constructed stimuli representing three taxonomic categories (people, manmade objects, and locations) and three thematic categories (school, medicine, and sports) and investigated the neural representations of these two dimensions using representational similarity analyses in human participants (10 men and 9 women). In specific regions of interest – the left anterior temporal lobe (ATL) and the left temporoparietal junction (TPJ) – we found that while both areas had significant effects of taxonomic information, the taxonomic relations had stronger effects in the ATL than in the TPJ (“doctor” and “teacher” closer in ATL neural activity), with the reverse for thematic relations (“doctor” and “stethoscope” closer in TPJ neural activity). A whole-brain searchlight analysis revealed that widely distributed regions, mainly in the left hemisphere, represented the taxonomic dimension. Interestingly, the significant effects of the thematic relations were only observed after the taxonomic differences were controlled for, in the left TPJ, the right superior lateral occipital cortex and other frontal, temporal and parietal regions. In summary, taxonomic grouping is a primary organizational dimension across distributed brain regions, with thematic grouping further embedded within such taxonomic structures.
How are concepts organized in the brain? It is well established that concepts belonging to the same taxonomic categories (e.g., “doctor” and “teacher”) share neural representations in specific brain regions. How concepts are associated in other manners (e.g., “doctor” and “stethoscope”, thematically related) remains poorly understood. We employed representational similarity analyses to unravel the neural representations of these different types of semantic relations by testing the same set of words that could be differently grouped by taxonomic categories or by thematic categories. We found that widely distributed brain areas primarily represented taxonomic categories, with the thematic categories further emended into taxonomic categories to be represented.
Introduction

The relations among concepts are critical elements of the semantic space. Numerous neuropsychological and neuroimaging studies have shown that the semantic-related concepts are represented by shared neural substrates (Rudrauf et al., 2008; Binder et al., 2009; Fairhall and Caramazza, 2013a) or induce similar neural activation patterns (Shinkareva et al., 2011; Devereux et al., 2013; Fairhall and Caramazza, 2013b; Simanova et al., 2014). However, most studies have only focused on taxonomic relations, where concepts sharing similar features belong to the same taxonomic categories (Rogers and McClelland, 2004; Binder et al., 2016). For example, “doctor” and “teacher” are both kinds of people; they share many more features relative to items from other taxonomic categories such as tools. “Doctor” is also semantically related to “stethoscope”, which is not based on feature similarity, but because they often co-occur in the same scenario or event. This relation is considered to be thematic (Estes et al., 2011). These two types of semantic relations constitute two major organizational dimensions of semantic contents, and unravelling the corresponding neural substrates is necessary to elucidate the neural mechanisms of semantic representation.

Previous neuroimaging and neuropsychological studies have failed to reach a consensus on the neural basis of taxonomic and thematic relations (see Mirman et al., 2017 for a review). Several studies have reported neuroanatomical dissociation between taxonomic and thematic relations, with the anterior temporal lobe (ATL) being sensitive to taxonomic representation and the temporoparietal junction (TPJ) being the reverse (Schwartz et al., 2011; Mirman and Graziano, 2012; Geng and Schnur, 2016). Others have reported different patterns: Some studies found effects in only one of these two regions (Kalénine et al., 2009; de Zubicaray et al., 2013; Lewis et al., 2015); Some found many other regions that were associated with either type of semantic relations but did not show a
clear convergence (Kotz et al., 2002; Sachs et al., 2008a; Sachs et al., 2008b; Kalénine et al., 2009; Kuchinke et al., 2009; Sass et al., 2009; Sachs et al., 2011; Anderson et al., 2014; de Zubicaray et al., 2014; Kalénine and Buxbaum, 2016); Some failed to detect any neural dissociations between these two types of relations (Jackson et al., 2015). Several factors have been considered to give rise to such discrepancies, such as the confounding factors of behavioural difference (Jackson et al., 2015), the semantic processing depth (Geng and Schnur, 2016) and the inconsistent definition of thematic relations (Mirman et al., 2017). Critically, these studies have predominantly employed univariate contrasts between the activation strengths in different conditions, which may mask effects where the two kinds of relations are represented through different activation patterns rather than overall activity strength. The only multivariate study (Anderson et al., 2014) focused on the whole-brain pattern without specific contrasts between the ATL and the TPJ.

Addressing these issues, we employed the representational similarity analysis (RSA) (Kriegeskorte et al., 2008; Mur et al., 2009) to unravel brain regions where concepts are related along taxonomic or thematic dimensions (Figure 1), with attention paid to behavioral differences, semantic tasks, and definitions of thematic relations. Nine sets of words were constructed across three taxonomic categories (people, manmade objects, locations) and three thematic categories (school, medicine, sports). Participants were instructed to explicitly access semantic information along both taxonomic and thematic dimensions in different runs. The trial-by-trial RT differences were controlled for. Theoretical representation dissimilarity matrix (RDMs) were constructed based on either of these two dimensions (e.g., the taxonomic RDM: doctor-teacher, 0, doctor-stethoscope, 1; the thematic RDM, doctor-teacher, 1, doctor-stethoscope, 0). The relations between these theoretical RDMs and the neural RDMs were examined in regional ROIs (the left ATL and TPJ), in a larger scale of potential neural encoding – modules of the semantic network (Xu et al., 2016), and in a whole-brain searchlight fashion. We specifically examined whether the two semantic dimensions had any
relatively unique effects.

Material and Methods

Participants. Twenty healthy Chinese native speakers (10 males; aged 18-27 years) participated in this study. All participants were right handed (measured by Chinese adaptation of (Oldfield, 1971)) and had normal or corrected-to-normal vision. All participants provided written informed consent. This study was approved by the Human Subject Review Committee at Peking University. One participant (female) was excluded from the analyses due to a technical dysfunction.

Stimuli. The stimuli set contained 45 Chinese words that belonged to nine conditions [3 taxonomic categories (people, manmade objects, and locations) × 3 thematic categories (school, medicine, and sports)]. Each condition had five words, including three bisyllabic (two characters) words and two trisyllabic (three characters) words, thus matching on number of syllables and characters across all conditions. Words across 3 taxonomic × 3 thematic categories were well matched on their visual complexity (stroke numbers between taxonomic categories: $F_{(2, 36)} = 0.09, p = 0.914$; between thematic categories: $F_{(2, 36)} = 0.92, p = 0.409$; interaction: $F_{(4, 36)} = 0.29, p = 0.881$ or logographeme numbers between taxonomic categories: $F_{(2, 36)} = 0.82, p = 0.449$; between thematic categories: $F_{(2, 36)} = 0.25, p = 0.782$; interaction: $F_{(4, 36)} = 0.61, p = 0.658$). To further make sure that any semantic condition effects were not attributable to potential confounding variables such as visual shape or word frequency, we carried out validation analyses (see Results section) including their matrices as covariates using Spearman’s rank partial correlation: the low-level visual dissimilarity matrix (Kriegeskorte et al., 2008; Devereux et al., 2013), in which each cell represented the mean pair-wised Jaccard distance between the binary silhouette images of words across conditions (i.e., mean of 25
word pairs in each pair of conditions); the word frequency dissimilarity matrix, in which each cell contained the mean pair-wised difference between the word frequency counts (Sun et al., 1997) across conditions. Finally, words in the sports condition, such as “award platform” and “audience”, tended to be associated with boarder thematic situations, we thus presented all words with pictures depicting the intended meanings in a familiarization phase, and performed further validation analyses excluding the sport condition (see Results section). Each word was visually presented in black “Song” bold, 36-point sized font at the center of a gray background. The viewing distance was 1.1 meters.

**Procedures.** Before the scanning, we had a warm-up session that presented each word with a picture of its intended meaning to familiarize the participants with the stimuli and to resolve potential ambiguities (see above). There were 10 runs during the scanning. Each run lasted 260 s. A 10 s blank screen was presented at the start and end of each run. All stimuli were presented once during each run. We first determined the sequence of the nine conditions in each run using the optseq2 optimization algorithm (Dale, 1999). The presenting orders of the five words within each condition were further randomized. The run orders were randomized across participants. Each trial started with a centrally presented fixation cross on a gray background for 500 ms, followed by the stimuli for 500 ms, and then a blank screen with varying lengths between 3 and 13 s, which were also defined using the optseq2 optimization algorithm. The participants were instructed to make semantic judgments (see below) in the subsequent 3500 ms following the onset of each stimulus. Both accuracy and reaction time were recorded. These procedures were implemented using E-prime 2.

**Tasks.** To ensure that the factor of the tasks did not bias the results, the participants were instructed to assess the meaning of these stimuli along both dimensions. In half of runs, a taxonomic judgment task was performed. The participants pressed the buttons with their right middle finger, right index finger and left index finger when the stimuli belonged to the taxonomic categories of man-made
objects, people and locations, respectively. In the other half of runs, the participants pressed the buttons with their right middle finger, right index finger and left index finger when the stimuli belonged to the thematic categories of medicine, school and sports, respectively. The sequence of the taxonomic and thematic runs was randomized across the participants.

Image acquisition. Imaging data were acquired using a MAGNETOM Prisma 3T MR scanner (Siemens, Erlangen, Germany) with 20-channel head-neck coil at the Centre for MRI Research, Peking University. High-resolution functional images were acquired using the simultaneous multi-slices echo planar imaging (SMS-EPI) sequence, the scanning plane is parallel to the straight gyrus, the phase encoding direction from posterior to anterior, repetition time (TR) = 2000 ms, echo time (TE) = 30 ms, flip angle (FA) = 90°, field of view (FOV) = 224 mm × 224 mm, matrix size = 112 × 112, 64 axial slices, slices thickness (ST) = 2 mm, gap = 0.2 mm, voxel size = 2 × 2 × (2 + 0.2) mm, multi-band factor = 2. High-resolution three-dimensional T1-weighted images were acquired using the magnetization-prepared rapid gradient-echo (MPRAGE) sequence, sagittal plane, TR = 2530 ms, TE = 2.98 ms, inversion time = 1100 ms, FA = 7°, FOV = 224 mm × 256 mm, matrix size = 224 × 256, interpolated to 448 × 512, 192 continuous sagittal slices, ST = 1 mm, voxel size = 0.5 × 0.5 × 1 mm.

Image preprocessing. The images were preprocessed using SPM12 (Wellcome Trust Center for Neuroimaging, http://www.fil.ion.ucl.ac.uk/spm/software/spm12/). Functional images were processed using procedures including first five volume exclusion, slice timing correction, and realignment to the individual’s first image of their first run using six rigid body transforming parameters. These resulting un-smoothed and un-normalized images were entered into the general linear model (GLM) at the individual level to maintain the original informative pattern across the voxels (Kriegeskorte et al., 2006). The GLM contains a regressor for each of these nine conditions,
along with six head motion regressors and a constant regressor for each run. To investigate the
effects of the type of semantic task on the neural representational patterns, we also built another
GLM in which the same stimuli conditions under different tasks (the taxonomic judgment task and
the thematic judgment task) were treated as different regressors. To control for potential confounding
effects of the reaction time (RT), we used the duration modulation method by convolving each trial
with a boxcar equal to the length of the trial’s RT for each participant (Grinband et al., 2008). A
high-pass filter cut-off was set as 128 s. To ensure maximal coverage of the anterior temporal lobe, a
lower threshold (10% of the mean global signal) was adopted as the implicit mask (Devereux et al.,
2013). To suppress the contribution of noisy voxels with high beta estimates due to high noise
(Misaki et al., 2010), the t-value image of each condition was calculated to capture the activation
patterns. The structure images were co-registered to the mean functional images and segmented into
different tissues. The resulting gray-matter probabilistic image of each participant was resliced into
functional images and thresholded at 1/3 to generate a binary mask for the searchlight-based RSA.
The forward and inverse deformation fields of each participant’s native space to the Montreal
Neurological Institute (MNI) space were also obtained in this step.

Multi-voxel pattern analyses (MVPA), RSA and multidimensional scaling (MDS) were implemented.
For any brain region at the MNI space, the images were first transformed to each participant’s native
space via inverse deformation fields and resliced to the same resolution as that of the functional
images.

RSA. The RSA was used to identify the representational content that emerged from the multivariate
activation patterns across the voxels in a given brain area (Kriegeskorte et al., 2008; Mur et al., 2009).
The representation of a brain area was characterized by the representational dissimilarity matrix
(RDM), which is a symmetric matrix indexed by these nine conditions horizontally and vertically in
the same order. Each element in this matrix measured the dissimilarity between the activation patterns in the two conditions across all voxels in that brain area. We use the Spearman’s rank correlation distance \((1 - \text{Spearman’s } r)\) to measure this dissimilarity. Then, the brain RDM was compared with multiple model RDMs by calculating the Spearman’s rank correlation across the elements within the lower triangle (not including the diagonal) or calculating the Spearman’s rank partial correlation to control for certain variables. The resulting correlation coefficients were Fisher-transformed and statistically inferred across participants. We mostly focused on two hypothetical model RDMs (Figure 1): the taxonomic RDM grouped by the taxonomic categories (e.g., teacher–doctor, 0; teacher–chalk, 1) and the thematic RDM grouped by the thematic categories (e.g., teacher–doctor, 1; teacher–chalk, 0). These two model RDMs were negatively correlated (Spearman’s \( r = -0.33 \)). The RSA results will reflect whether the neural patterns associated with the taxonomic RDM or the thematic RDM.

**MDS.** An MDS analysis was implemented to provide a visualization of the representational patterns of a particular brain region. For any given brain region, an MDS analysis was applied on the mean neural RDM across participants using the PROXSCAL procedure (Busing et al., 1997) in SPSS Statistics 22. The PROXSCAL performs multidimensional scaling of proximity data to find a least-square representation of the objects in a low-dimensional space by minimizing the normalized raw stress. Ten thousand random starts were configured, and the configuration with the lowest normalized raw stress was used as the initial configuration.

**ROI definition.** We focused on two anatomically defined ROIs: the left ATL and the left TPJ. The left ATL was defined as the union set of the following six sub-regions according to the Harvard-Oxford Atlas (probability > 0.2): the temporal pole (TP), the anterior superior temporal gyrus (aSTG), the anterior middle temporal gyrus (aMTG), the anterior inferior temporal gyrus (aITG), the anterior
temporal fusiform cortex (aTFC), and the anterior parahippocampal gyrus (aPHG) (Figure 2A; Figure 3A). These areas cover the regions of Brodmann area (BA) 38 and the anterior portions of BA 20 and BA 21, in which taxonomic errors are localized (Schwartz et al., 2011). The left TPJ was defined as the union of the posterior supramarginal gyrus (pSMG) and the angular gyrus (AG) in the Harvard-Oxford Atlas (probability > 0.2) (Figure 2A; Figure 3D). These areas cover the regions of BA 39 and the adjacent supramarginal gyrus, in which thematic errors are localized (Schwartz et al., 2011). To determine whether different sub-regions in the left ATL and the left TPJ varied, we also investigated the representational patterns in each sub-region of the two regions separately. Because the ATL is adjacent to the air-bone interface that leads to inhomogeneities in the magnetic field, we computed the temporal signal to noise ratio (tSNR) in each sub-region of the ATL for each participant using the motion-corrected unsmoothed images in the native space. The tSNR was calculated by dividing the mean of the time series across the whole run by its standard deviation (Murphy et al., 2007). The mean tSNR over all voxels within a sub-region and over all the runs represented the tSNR of that sub-region.

**Whole-brain searchlight.** A whole-brain searchlight-based RSA was implemented under the framework of Kriegeskorte et al. (2006) to identify brain areas that locally represent taxonomic and thematic relations and their unique information. A whole-brain searchlight was implemented within the individual gray-matter mask generated in the preprocessing stage. For each voxel, a 6 mm-radius sphere was built (including 113 voxels), and the activity patterns of these voxels across different conditions were extracted to build the neural RDM. These neural RDMs were correlated with model RDMs, and the Fisher-transformed Spearman’s correlation coefficient was returned to this voxel. The resulting similarity maps of each participant were normalized to the MNI space using the forward deformation field and were spatially smoothed using a 6-mm full-width at half maximum (FWHM) Gaussian kernel. A group level random-effect analysis was then implemented across these maps using
the permutation-based nonparametric method (Nichols and Holmes, 2002) with SnPM 13 (http://warwick.ac.uk/snpm). No variance smoothing was used, and 10,000 permutations were performed. A conventional cluster-extent based inference threshold (voxel-level at \( p < 0.001; \) cluster-extent FWE \( p < 0.05 \)) was adopted, and we stated explicitly when more stringent or moderate thresholds were applied. We also performed searchlight analyses using spheres with radii of 4 mm, 8 mm, and 10 mm. The results using the different sized spheres were very similar to each other with the tendency that the effects became stronger as the radius increased.

Given that participants were instructed to press different buttons according to taxonomic or thematic categories in the taxonomic and thematic judgement tasks respectively, the effect of button-press inevitably confounded the taxonomic and the thematic effects in the corresponding task. To exclude the confounding factors of button-press, we did the following analyses. (1) We localized effects that are associated with button-press across tasks. The model RDM of button press was defined as the rank variables according to whether the participants pressed the button using the same hand and finger (same hand, same finger: 0; same hand, different finger: 1; different hand, different finger: 2). Thus, the taxonomic task and the thematic task had different button-press RDMs. They were anticorrelated (Spearman’s \( r = -0.22 \)) and roughly corresponded to the taxonomic RDM in the taxonomic task and the thematic RDM in the thematic task. We correlated these two button-press RDMs with the neural representational pattern in their corresponding tasks. The button-press effect should be the common areas of these two correlations. Any clusters with semantic RSA effects overlapping with these areas should be excluded. (2) We further validated the main results with an additional analysis in a cross-task-and-condition fashion. That is, we carried out the RSA using the taxonomic RDM correlated with the neural activity pattern in the thematic tasks and using the thematic RDM correlated with the neural activity pattern in the taxonomic tasks. Since the button-press RDM of one semantic
task was not positively correlated with the semantic RDM in the other type (Spearman’s $r = -0.27$), the effects of button-press would not confound the semantic relation effects.

**Semantic sub-network definition.** For regions that are consistently activated during semantic tasks (Binder et al., 2009), based on the topological structures of their connections, Xu et al. (2016) identified three intrinsic semantic subnetworks, including a “semantic-DMN module” and a “semantic-PSN module” that were hypothesized to support semantic representation. Masks of these two modules were adopted based on the voxel-wised results under a connectivity density of 0.4 in that paper (Figure 5A). The semantic-DMN sub-network primarily includes the bilateral retrosplenial cortices/posterior cingulate cortices/precuneus, bilateral medial prefrontal cortices, bilateral posterior angular gyrus extending to the transverse occipital sulcus, the left superior frontal gyrus, and the middle part of the left fusiform gyrus/parahippocampal cortex. The semantic-PSN sub-network primarily includes the left ventral frontal cortices, the entire length of the left middle temporal cortices, and the left temporoparietal junction.

**Brain visualization.** The brain results were mapped onto the inflated surface of the PALS-B12 atlas (Van Essen, 2005) using Caret (http://brainvis.wustl.edu/wiki/index.php/Caret:Download). We used the average fiducial map to display the whole-brain searchlight results.

**Results**

**Behavioral results.** The mean and standard deviation of reaction time (RT) and accuracy in each condition is presented in Table 1. We performed 2 tasks × 3 taxonomic × 3 thematic categories repeated measures ANOVA. Regarding accuracy, analyses using the arcsine transformed accuracy
data revealed no significant effects of any main effects, or three-way interactions ($P_s > 0.05$).

Regarding the RT, there was no significant effect of tasks or three-way interactions ($P_s > 0.1$), but significant main effects of taxonomic categories ($F_{(2, 27)} = 10.42, P = 0.001$, Greenhouse-Geisser corrected for the degrees of freedom) and of thematic categories ($F_{(2, 36)} = 3.41, P = 0.044$).

To exclude the potential confounding effect of the trial-by-trial RT difference (Yarkoni et al., 2009; Todd et al., 2013), we used the duration modulation method (Grinband et al., 2008) in the subsequent brain analyses (see the Material and Methods section); To exclude the potential confounding effect of the accuracy differences across conditions on RSA, we implemented a validation analysis, using the Spearman partial correlation to control for the accuracy-RDMs of individual participants, in which each cell represented the pair-wise accuracy differences between conditions (see the section of the “validation analyses” below).

Taxonomic and thematic representation in the left ATL and left TPJ. We first investigated the representational patterns in two anatomically defined ROIs – the left ATL and left TPJ (Figure 2A).

The left ATL was primarily organized by taxonomic dimension and modulated by thematic dimension.

As shown in Figure 2B, the RSA revealed that the neural response pattern in the left ATL was significantly correlated with the taxonomic RDM (mean Fisher transformed Spearman’s $r = 0.24$; $t_{(18)} = 4.80, P < 0.001$) and not with the thematic RDM (mean $r = 0.01$; $t_{(18)} = 0.24, P = 0.817$). The strength of its correlation with the taxonomic RDM was significantly stronger than that with the thematic RDM (paired $t_{(18)} = 2.76, P = 0.013$). After controlling for the thematic difference using Spearman’s rank partial correlation, the taxonomic effect remained significant (partial correlation, mean $r = 0.25$; $t_{(18)} = 5.91, P < 0.001$); after controlling for the taxonomic difference, the thematic effect became significant (partial correlation, mean $r = 0.09$, $t_{(18)} = 2.87, P = 0.010$). The MDS results also
illustrated that the representational pattern in the left ATL was largely grouped by the taxonomic dimension (Figure 2E, left; Normalized Raw Stress = 0.092, Stress-I = 0.303, Stress-II = 0.942, S-Stress = 0.246).

Analyses within different sub-regions of the left ATL showed that all sub-regions represented taxonomic information (mean r: 0.11-0.21; one sample t-test against zero, Bonferroni corrected ps < 0.03), but not thematic information (mean r: -0.01-0.01; one sample t-test against zero, uncorrected ps > 0.41) (Figure 3C). A 6 sub-regions × 2 types of semantic information (taxonomic and thematic information) repeated measures ANOVA revealed a significant effect of semantic information (F (1, 18) = 9.17, p = 0.007), but not the main effect of sub-regions (F (5, 90) = 1.938, p = 0.096) or the interaction between sub-regions and semantic information (F (5, 90) = 0.48, p = 0.790). After controlling for the thematic difference, all sub-regions in the left ATL continued to have significant effects of taxonomic information (partial correlation, mean r: 0.12-0.23; one sample t-test, Bonferroni corrected ps < 0.02).

After controlling for the taxonomic difference, some sub-regions in the left ATL, i.e., the aSTG, the aMTG, and the aPHG, showed trends of thematic information effect (partial correlation, mean r: 0.07 in aSTG, 0.07 in aMTG, and 0.10 in aPHG; one sample t-test, uncorrected ps < 0.04) that did not survive the Bonferroni correction. We also calculated the tSNR in each sub-region in the left ATL (Figure 3B). The semantic information across subregions here did not seem to be fully associated with tSNR: The correlation between the tSNR and the amount of semantic information (sum of the RSA value of both taxonomic and thematic effects) across regions were not significant (Spearman’s r = 0.37, p = 0.47); subregions such as aPHG had low tSNR yet trends of greater amount of semantic information.

The left TPJ represented taxonomic and thematic information equally. As shown in Figure 2C, the RSA results showed that the neural response pattern in the left TPJ was significantly correlated with
both the taxonomic RDM (mean r = 0.15; t(18) = 3.60, p = 0.002) and the thematic RDM (mean r = 0.09; t(18) = 2.30, p = 0.034), without significant differences between these two effects (paired t(18) = 0.82, p = 0.422). After controlling for the thematic difference, the taxonomic effects remained significant (partial correlation, mean r = 0.20; t(18) = 5.53, p < 0.001), and after controlling for the taxonomic difference, the thematic effect was also significant (partial correlation, mean r = 0.15; t(18) = 4.75, p < 0.001). The MDS results also illustrated that the representational pattern in the left TPJ appeared to reflect both taxonomic and thematic dimensions (Figure 2E, right; Normalized Raw Stress = 0.089, Stress-I = 0.299, Stress-II = 0.928, S-Stress = 0.238).

Analyses in different sub-regions within TPJ also showed that the pattern observed using the whole TPJ was rather homogeneous, with no significant differences across various sub-regions (Figure 3E).

Both the left pSMG and the left AG activity patterns contained taxonomic (mean r = 0.14 in pSMG, mean r = 0.17 in AG; one sample t-test, ps ≤ 0.002) and thematic information (mean r = 0.09 in pSMG, mean r = 0.06 in AG; one sample t-test, ps < 0.057). The 2 sub-regions (the left pSMG and the left AG) × 2 types of semantic information (taxonomic and thematic information) repeated measures ANOVA did not reveal any significant effects (main effect of sub-regions: F(1, 18) = 1.48, p = 0.240; main effect of types of semantic information: F(1, 18) = 0.08, p = 0.781; interaction between regions and types of semantic information: F(1, 18) = 1.77, p = 0.200). After controlling for the thematic difference, both sub-regions showed effects of taxonomic information (partial correlation, mean r = 0.18 in pSMG, mean r = 0.21 in AG; one sample t-test, ps < 0.001). After controlling for the taxonomic difference, both sub-regions also showed effects of thematic information (partial correlation, mean r = 0.15 in pSMG, mean r = 0.13 in AG; one sample t-test, ps ≤ 0.001).

Comparisons between the left ATL and TPJ. Figure 2D displays the results of the direct comparisons between the two ROIs. A 2 regions (left ATL and left TPJ) × 2 types of semantic dimension
(taxonomic and thematic information) repeated measures ANOVA revealed a significant interaction
(F (1,18) = 7.87, p = 0.012). The main effect of types of semantic dimension was marginally significant
(F (1, 18) = 3.79, p = 0.067) and the main effect of regions was not (F (1, 18) = 0.004, p = 0.953). The post
hoc analyses revealed that the left ATL carried more taxonomic information than the left TPJ (Paired t
(18) = 2.61, p = 0.018), while the left TPJ carried more thematic information than the left ATL (Paired t
(18) = 2.48, p = 0.023). Although the tSNR of the ATL was significantly lower than that of the TPJ
(mean-ATL = 22.64, mean-TPJ = 44.85; paired t (18) = 31.3, p < 0.001), such tSNR difference could not
explain the interaction effect between semantic relations and regions. That is, it is not clear why low
tSNR in the ATL would heighten the sensitivity to detect one type of semantic relation and
compromise the other.

Whole-brain searchlight. To explore the effects of brain regions beyond the left ATL and the left TPJ,
we implemented a whole-brain RSA-based searchlight analyses (Kriegeskorte et al., 2006) to uncover
any brain areas whose representational pattern significantly correlated with the taxonomic or thematic
RDM (Figure 4).

Button press. As participants pressed different buttons according to the taxonomic or thematic tasks
in the scanner, the effect of button-press inevitably confounded with the taxonomic effect in the
taxonomic task (i.e., button press fingers aligned with taxonomic conditions) and the thematic effects
in the thematic task (i.e., button press fingers aligned with thematic conditions). To exclude this
confounding factor, we first specified what regions associated with the button-press by looking at the
RSA results with the button-press RDMs that were common to the two tasks (see Material and
Methods section). At the conventional threshold (primary voxel-level threshold p < 0.001 and
cluster-level PFWE-Corr < 0.05), we found that the button-press effect was confined in the primary
motor cortex, the primary somatosensory cortex, and the secondary somatosensory cortex. These
areas are outlined with black contours in Figure 4. In the following analysis, clusters showing semantic-relation effects (taxonomic or thematic) that overlapped with these regions would not be considered.

*Distributed brain regions representing taxonomic information.* Under the conventional threshold (primary voxel-level threshold \( p < 0.001 \) and cluster-level \( \text{PFWE-Corr} < 0.05 \)) the effects of taxonomy were extremely robust, covering much of the temporal, parietal, frontal, and occipital cortex. We thus raised the threshold to a more stringent one (voxel-level \( \text{PFWE-Corr} < 0.05 \), clusters size > 1000 mm\(^3\)). As shown in Figure 4A (see also Table 2) the neural activity pattern in distributed left-hemispheric areas significantly associated with the taxonomic RDM, including the temporo-occipital part of the middle and inferior temporal gyrus that extended to the inferior part of the lateral occipital cortex, the superior division of the lateral occipital cortex centered in the transverse occipital sulcus, the posterior division of the fusiform gyrus, and the precuneus region located between the calcarine cortex and the posterior cingulate gyrus. After controlling for the thematic difference using Spearman’s rank partial correlation, the taxonomic effect became stronger in similar regions (higher voxel t-values and larger clusters; Figure 4B, Table 2, voxel-level \( \text{PFWE-Corr} < 0.05 \) and clusters size > 1000 mm\(^3\)) and additionally included bilateral subcallosal cortices, bilateral intracalcarine cortices that extended to lingual gyri, the left middle frontal gyrus that extended to the superior frontal gyrus, the left middle frontal gyrus that extended to the triangular part of the inferior frontal gyrus, the right anterior insula cortex that extended to the frontal operculum cortex, the right occipital-fusiform gyrus, the left superior division of the lateral occipital cortex that extended to the superior parietal lobule.

Regions that represented thematic information emerged only after controlling for the taxonomic difference. Correlating the neural activity pattern with the thematic RDM in the whole-brain
searchlight yielded significant clusters only in the areas associated with button-press effects at the same threshold (Figure 4C; primary voxel-level threshold $p < 0.001$ and cluster-level $\text{PFWE-Corr} < 0.05$).

After controlling for the taxonomic RDM, significant thematic effects emerged in widely distributed regions across the occipital, frontal, temporal and parietal cortices (Figure 4D, Table 3; primary voxel-level threshold $p < 0.001$ and cluster-level $\text{PFWE-Corr} < 0.05$).

**Taxonomic and thematic representation at the semantic sub-network level.** Beyond the regional level, we examined the representational patterns in regions that formed two topologically dissociable semantic sub-networks, i.e., the semantic-DMN sub-network and the semantic-PSN sub-network (Xu et al., 2016) (Figure 5A).

As shown in Figure 5B, the RSA result showed that the activity pattern in the **semantic-DMN sub-network** significantly correlated with the taxonomic RDM (mean $r = 0.24$; $t(18) = 5.48$, $p < 0.001$) and not with the thematic RDM (mean $r = 0.03$, $t(18) = 1.00$, $p = 0.332$), with significant differences between these two effects (paired $t(18) = 3.362$, $p = 0.003$). After controlling for the thematic difference, the activity pattern in the semantic-DMN sub-network remained significantly correlated with the taxonomic RDM (mean $r = 0.27$, partial correlation, $t(18) = 6.292$, $p < 0.001$), and after controlling for the taxonomic difference, became significantly correlated with the thematic RDM (partial correlation, mean $r = 0.12$, $t(18) = 4.281$, $p < 0.001$). These results indicated that the activity pattern in the semantic-DMN sub-network was primarily organized by taxonomic information and secondarily organized by thematic information.

As shown in Figure 5C, the RSA results of the **semantic-PSN sub-network** was similar to that in the semantic-DMN sub-network. The neural activity pattern in the semantic-PSN sub-network significantly correlated with the taxonomic RDM (mean $r = 0.25$; $t(18) = 4.94$, $p < 0.001$) and not with...
the thematic RDM (mean r = 0.04; $t_{(18)} = 1.26$, $p = 0.223$), with significant difference between the strengths of these two effects (paired $t_{(18)} = 2.66$, $p = 0.016$). After controlling for the thematic difference, the taxonomic effects remained significant (mean r = 0.28; partial correlation, $t_{(18)} = 6.08$, $p < 0.001$), and after controlling for the taxonomic difference, the thematic effects also became significant (partial correlation, mean r = 0.13; $t_{(18)} = 4.88$, $p < 0.001$).

When directly comparing the amount of taxonomic and thematic information carried by these two sub-networks (Figure 5D) using a 2 (DMN vs. PSN semantic sub-networks) $\times$ 2 (taxonomic vs. thematic information) repeated measures ANOVA, a significant main effect was observed only for the semantic relations ($F_{(1, 18)} = 10.15$, $p = 0.005$). There was neither the main effect of semantic sub-networks ($F_{(1, 18)} = 0.52$, $p = 0.481$) nor interaction ($F_{(1, 18)} = 0.02$, $p = 0.884$), suggesting the similar representational structure in terms of taxonomic and thematic dimensions in these two sub-networks.

The modulation effects by the task goals. Finally, we assessed the degree to which the activity pattern in these semantic-related areas (the left ATL, the left TPJ, the semantic-DMN sub-network, and the semantic-PSN sub-network) changed according to different semantic tasks (Figure 6). A 2 (taxonomic vs. thematic judgment tasks) $\times$ 2 (taxonomic vs. thematic information) repeated measures ANOVA revealed no significant effects of semantic tasks ($p_s \geq 0.352$), a significant main effect of semantic relation type in the left ATL, the semantic-DMN sub-network and the semantic-PSN sub-network ($p_s \leq 0.013$; marginally significant in the left TPJ, $F_{(1, 18)} = 3.26$, $p = 0.088$), and a significant interaction in all regions/systems ($p_s \leq 0.001$). The post hoc analyses revealed that in all regions the taxonomic effects were stronger in the taxonomic judgment task than the thematic judgment task (paired t-test, $p_s \leq 0.002$) and the thematic effects were stronger in the thematic judgment task than the taxonomic judgment task (paired t-test, $p_s \leq 0.013$).
Validation analyses. We carried out four validation analyses to exclude the potential effects of confounding factors: (1) Words in the thematic category of sports tended to have lower prototypicality and were associated with a broader domain (see the Material and Methods section), we excluded the thematic category of sports and repeated the ROI and sub-network analyses; (2) We further excluded the behavioral accuracy differences by repeating all the ROI and sub-network analyses using the Spearman partial correlation and included the accuracy-RDMs of individual participants as covariate; (3) We further regressed out two control matrices (the word frequency and the visual similarity matrices; see the Material and Methods section) in the RSA. (4) In another attempt to fully exclude the confounding effects of button-press in the whole brain searchlight analyses, we carried out an additional analysis by correlating the taxonomic RDM with the neural activity pattern in the thematic task (i.e., button press fingers aligned with thematic conditions) and correlating the thematic RDM with the neural activity pattern in the taxonomic task (i.e., button press fingers aligned with taxonomic conditions). In the ROI and sub-network analyses, the result patterns in all these validation analyses were similar to those in the main analysis. In the whole searchlight analyses, the taxonomic effects (in the thematic judgment task) were mainly found in the left temporooccipital part of the inferior and middle temporal gyrus, the precuneus, and the right anterior medial temporal lobe (primary voxel-level threshold p < 0.001 and cluster-level pFWE-Corr < 0.05); These effects became stronger and involved more regions when the thematic differences were controlled for. The thematic effects (in the taxonomic judgment task) only appeared when the taxonomic differences were controlled for, which mainly fell in bilateral superior occipital gyri, bilateral temporoparietal junctions, the right superior and middle frontal gyrus, the precuneus, the anterior cingulate and the adjacent paracingulate gyrus, the left posterior parahippocampal gyrus, the ventral occipital/lingual/fusiform gyri (p < 0.001, uncorrected, cluster size > 20 voxels). Overall, both the taxonomic-specific effects and the thematic-specific effects fell into similar regions as those reported in the main results.
Using the RSA, we elucidated the brain regions in which words were organized along taxonomic ("doctor" and "teacher" closer) or thematic ("doctor" and "stethoscope" closer) dimensions. As summarized in Table 4, we found a left-lateralized distributed network that primarily respected words’ taxonomic structures. This network mainly included the ATL, the TPJ, the tempororooccipital part of the middle and inferior temporal gyrus that extended to the inferior part of the lateral occipital cortex, the superior division of the lateral occipital cortex centered in the transverse occipital sulcus, the posterior division of the temporal fusiform cortex, and the precuneus cortex. By contrast, the effects of thematic relations were directly observed only in the left TPJ in the ROI analysis, and emerged in many other regions, including the ATL, after the taxonomic difference was controlled for. The same pattern was observed when looking at a larger system level – the neural response pattern of each of the two semantic-subnetworks was primarily associated with the taxonomic RDM, and showed association with the thematic RDM after the taxonomic difference was controlled for. That is, the primary organization dimension for concepts appears to be taxonomic categories, with thematic categories only embedded within the taxonomic structure.

The regions showing effects of taxonomic organization corresponded well to the literature where such taxonomic dimension was examined using MVPA/RSA (Shinkareva et al., 2011; Devereux et al., 2013; Fairhall and Caramazza, 2013b; Clarke and Tyler, 2014; Simanova et al., 2014), and were also in accord with the vast literature showing taxonomic-category-preferring activities using univariate approaches for the three taxonomic categories used here – people, manmade objects, and locations (Binder et al., 2009; Fairhall and Caramazza, 2013a). The observations that the left TPJ, not the left
ATL, primarily showed a significant correlation with the thematic organization, is consistent with the neuropsychological studies showing that lesions in the left TPJ were relatively specifically associated with thematic errors (Schwartz et al., 2011).

Different from the previous studies, however, we found that the activity patterns in regions that are classically viewed to respect taxonomic categories, e.g., the left ATL, the left transverse occipital sulcus and the precuneus, actually further respect the thematic dimension once the taxonomic difference was controlled for. That is, thematic relations appear to be embedded within the taxonomic structure rather than being represented by separate brain regions. The concepts are firstly organized by taxonomic categories of people, manmade objects, and locations. Additionally, across different taxonomic categories, there are further effects of thematic association – “doctor” and “stethoscope” are represented in a more similar pattern than “doctor” and “chalk”. On a larger scale, two semantic subsystems that were parcellated based on modularity structures of the resting-state semantic network (Xu et al., 2016) were examined. They encompassed brain regions that tend to be more relevant for multimodal experiential and language-supported semantic encoding, respectively (Xu et al., 2017). The results showed that in both subsystems taxonomic information was the primary dimension and thematic relations were further embedded within the taxonomic structures. The exact mechanisms for both systems in respecting primarily the taxonomic relation remain to be further spelled out.

Cognitively, taxonomic and thematic relations have been hypothesized to reflect different kinds of representational mechanisms (Estes et al., 2011): The taxonomic relation is primarily based on the similarity of semantic features (i.e., various types of sensorimotor properties); the thematic relation is based on the concurrence and complementary relations in the same event. Our findings that most regions represented both types of semantic relations suggest that there might be a general neural representational mechanism underlying both taxonomic and thematic relations (see discussions in
Jackson et al., 2015). One possibility is that the thematic co-occurrence is one type of “semantic features” or results from the integration of several particular types of semantic features, such as space, time, and action (see below). Because the neural representational pattern may reflect the overall similarity of semantic features, the taxonomic relation, which is based on the similarity in the majority of semantic features (i.e., various types of sensorimotor features), appears much stronger than the thematic relation, which is based on the similarity in fewer types of semantic features. Given that space and action are central to forming an event, brain areas relating to spatial and action-related semantic feature processing is likely to be involved in thematic representation. This may explain why the effects of thematic organization are most transparent in the TPJ. The TPJ is centered between the transverse occipital sulcus, which plays an important role in the cognition of scenes (Dilks et al., 2013), and the posterior temporal lobe and the rostral part of the inferior parietal lobe, which are involved in motion and action cognition (Iacoboni and Dapretto, 2006). The area with the strongest thematic effects (after taxonomic differences were controlled for) in the whole brain searchlight analyses – the right superior lateral occipital cortex that is adjacent to the parietal cortex – is also found to be involved in visuospatial processing (Goodale and Milner, 1992; Mellet et al., 1995). Lesions to the bilateral occipitoparietal lobes lead to simultanagnosia, a syndrome characterized by the restricted attention window to only one object at a time and the failure to comprehend the overall meaning of a scene (Bälint, 1909; Dalrymple et al., 2013). Furthermore, the involvement of the dorsal visual system in thematic processing is in line with the recent finding in a word-to-picture eye-tracking study, where earlier activation was found on thematically related objects as compared to functionally related items (Kalénine et al., 2012).

It is also worth considering whether the asymmetric organization, that the thematic associations are embedded in the taxonomic structures, could also be explained by different manners of neural coding. The taxonomic relation, which is based on the integration of sensorimotor features, may rely on the
distributed coding of large populations of neurons, a coding paradigm which has widely been found to represent sensorimotor information (Georgopoulos et al., 1986; Georgopoulos et al., 1988). The thematic relation, on the other hand, is built on the co-firing concepts with less overlapping sensorimotor features in the same time/space sharing event, and might be better captured by sparse neuronal coding or associations/connections across the conceptual representations (Binder, 2016). In line with these assumptions, it has been reported that the concept cell-assemblies in the medial temporal lobe encode semantic associations in a sparse manner (Quiroga, 2012; De Falco et al., 2016). Also, the MVPA study by Anderson et al. (2014) showed that when the whole-brain activity pattern was used to predict various concrete concept conditions, the leave-one-domain-out taxonomic predictions had better performances than the leave-one-taxonomic-category-out domain-related predictions, indicating that the taxonomic information was better captured by the whole brain activity pattern. How such population- vs. sparse- (overlapping vs. association) coding of taxonomic vs. thematic relations could explain the current findings remains to be further explored.

Our results showed a significant effect of task modulation for both dimensions in our regions/sub-networks of interest, with effects of a semantic dimension heightened in the task judging that dimension compared to the task judging the other dimension. This result is consistent with the line of findings that neural activity patterns may be modulated by task-related attention (Stokes et al., 2009; Chiu et al., 2011; Hjortkjær et al., 2017; Nastase et al., 2017). Regarding semantic processing, however, some previous studies have suggested or theoretically postulated that the neural representation pattern in only the frontoparietal regions (Bracci et al., 2017) or the integrative layer between the semantic control areas and the semantic representational areas (Ralph et al., 2016) are affected by the semantic tasks. The effects and mechanisms of task goal modulation warrant further understanding.
To conclude, we observed widely distributed brain areas that primarily organize conceptual representation along taxonomic structures, with thematic relations further embedded in the taxonomic categories. Only in the TPJ thematic effects were as strong as the taxonomic effects, which might be related to its relevance in semantic features that are central to thematic event formation such as space and action. This shared brain system for taxonomic and thematic dimensions may reflect a unified feature-based integration mechanism for different types of semantic relations.
Reference


Stokes M, Thompson R, Nobre AC, Duncan J (2009) Shape-specific preparatory activity mediates attention to targets in...


Table 1. Accuracy (ACC) and reaction time (RT) data (mean ± SD).

<table>
<thead>
<tr>
<th>Taxonomic Categories</th>
<th>Thematic Categories</th>
<th>Taxonomic Judgment Tasks ACC (%)</th>
<th>RT (ms)</th>
<th>Thematic Judgement Tasks ACC (%)</th>
<th>RT (ms)</th>
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<td>1460 ± 420</td>
<td>95 ± 7</td>
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Table 2: Whole-brain searchlight results of the taxonomic effects (voxel-level PFWE-Corr < 0.05, clusters with sizes > 1000 mm\(^3\). Clusters that overlapped with the regions associated with the button-press effect were excluded. Regions are labelled according to the Harvard-Oxford cortical and subcortical atlas).

<table>
<thead>
<tr>
<th>Anatomical Label</th>
<th>Peak Voxel (T Value)</th>
<th>Cluster Size (Voxels)</th>
<th>PFWE-Corr (Voxel Level)</th>
<th>MNI Coordinates</th>
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Table 3: Whole-brain searchlight results of the thematic effects (primary voxel-level threshold $P < 0.001$ and cluster-level $\text{PFW-E-Corr} < 0.05$. Clusters that overlapped with the regions associated with the button-press effect were excluded. Regions are labelled according to the Harvard-Oxford cortical and subcortical atlas).

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<th>$\text{PFW-E-Corr}$ (Cluster Level)</th>
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<td>R Insular Cortex</td>
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<tr>
<td>R Occipital Fusiform Gyrus</td>
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<tr>
<td>L Lingual Gyrus</td>
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<td></td>
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<tr>
<td>R Lateral Occipital Cortex, inferior division</td>
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<td>R Cingulate Gyrus, posterior division</td>
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### Table 4. A schematic result summary

<table>
<thead>
<tr>
<th>ROIs</th>
<th>Taxonomic Effects</th>
<th>Thematic Effects</th>
<th>Taxonomic Effects After Controlling for Thematic Difference</th>
<th>Thematic Effects After Controlling for Taxonomic Difference</th>
<th>Modulated by Task Demands</th>
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<td>ATL</td>
<td>++++</td>
<td>-</td>
<td>++++</td>
<td>++</td>
<td>√</td>
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<tr>
<td>TPJ</td>
<td>+++</td>
<td>++</td>
<td>+++</td>
<td>+++</td>
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<tr>
<td>Whole-brain Searchlight&lt;sup&gt;b&lt;/sup&gt;</td>
<td>ITG/MTG/LO, TOS, precuneus, fusiform (see Table 2)</td>
<td>-</td>
<td>ITG/MTG/LO, TOS, precuneus, fusiform, and other brain areas (see Table 2)</td>
<td>LO, PTO, and other brain areas (see Table 3)</td>
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<tr>
<td>Semantic Subnetworks</td>
<td>DMN</td>
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<td>-</td>
<td>++</td>
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<td>PSN</td>
<td>+++</td>
<td>-</td>
<td>+++</td>
<td>++</td>
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</tbody>
</table>

ITG = inferior temporal gyrus; MTG = middle temporal gyrus; LO = lateral occipital; TOS = transverse occipital sulcus; PTO = parietal-temporal-occipital association areas

<sup>a</sup>: Number of the plus signs indicate relative strength.
<sup>b</sup>: In the whole-brain searchlight analyses, the thematic effects emerged only after controlling for the taxonomic difference.
<sup>c</sup>: The tick mark indicate that the neural representational pattern can be modulated by task goals, i.e., in the taxonomic task, the area represented more taxonomic information, and in the thematic task, the area represented more thematic information.
Figure Captions:

**Figure 1. Experimental design.** A. The procedures in a trial. Each trial started with a fixation cross on a gray background for 500 ms, followed by the stimuli for 500 ms, and then a blank screen lasting between 3 and 13 s. This interval was defined using optseq2 (Dale, 1999). B. Stimuli. Forty-five words were used; the words were organized into nine conditions (3 taxonomic × 3 thematic categories). C. The hypothetical representational dissimilarity matrix (RDM). The taxonomic RDM was grouped by taxonomic relations, and the thematic RDM was grouped by thematic relations. They were negatively correlated.

**Figure 2. Representational pattern in the left ATL and the left TPJ.** A. The spatial layout of the left ATL (yellow) and the left TPJ (cyan). The areas were anatomically defined according to the Harvard-Oxford Atlas. B. The RSA results in the left ATL. C. The RSA results in the left TPJ. D. Direct comparison of the RSA results in the left ATL and those in the left TPJ. In B, C, and D, the bars with solid colors indicate the Fisher transformed Spearman’s rank correlation between the representational patterns and the taxonomic RDM or the thematic RDM. The bars with stripes indicate the Fisher transformed Spearman’s rank partial correlation between the representational patterns and the taxonomic RDM or the thematic RDM after controlling for the thematic or taxonomic differences. *: p < 0.05. Error bar: ± standard error. E. MDS results of the representational patterns in the left ATL (yellow border) and the left TPJ (the cyan border). Different shapes indicate different taxonomic categories, while different colors indicate different themes.

**Figure 3. Representational pattern in different sub-regions in the left ATL and TPJ.** A. The spatial layout of the different sub-regions in the left ATL. The regions were anatomically defined according to the Harvard-Oxford Atlas. B. The TSNR of different sub-regions in the left ATL. C. The RSA results in different sub-regions in the left ATL. *: p < 0.05, Bonferroni corrected. Error bar: ± standard error. D. The spatial layout of the different sub-regions in the left TPJ. The regions were anatomically defined according to the
Figure 4. Whole-brain searchlight results. A. Taxonomic effects. Voxel-level PFWE-Corr < 0.05, clusters with sizes smaller than 1000 mm$^3$ are not shown. B. Taxonomic effects after controlling for the thematic differences. Voxel-level PFWE-Corr < 0.05, clusters with sizes smaller than 1000 mm$^3$ are not shown. C. Thematic effects. Primary voxel-level threshold p < 0.001 and cluster-level PFWE-Corr < 0.05. D. Thematic effects after controlling for the taxonomic differences. Primary voxel-level threshold p < 0.001 and cluster-level PFWE-Corr < 0.05. The areas that outlined in black line contours were associated with button-press (primary voxel-level threshold p < 0.001 and cluster-level PFWE-Corr < 0.05).

Figure 5. Representational pattern of the semantic-DMN sub-network and semantic-PSN sub-network. A. The spatial layout of the DMN sub-network (red) and the PSN sub-network (green). These semantic sub-networks were defined by Xu et al., (2006). B. The RSA results of the semantic-DMN sub-network. C. The RSA results of the semantic-PSN sub-network. D. Direct comparison of the RSA results of the semantic-DMN sub-network and those of the semantic-PSN sub-network. The bars with solid colors indicate the Fisher transformed Spearman’s rank correlation between the representational patterns and the taxonomic RDM or the thematic RDM. The bars with stripes indicate the Fisher transformed Spearman’s rank partial correlation between the representational patterns and the taxonomic RDM or the thematic RDM after controlling for the thematic or taxonomic differences. *: p < 0.05. N.S: not significant. Error bar: ± standard error.

Figure 6. Task modulation effects of neural representational patterns. The Fisher transformed Spearman’s rank correlation between the representational patterns in each neural substrate and the taxonomic RDM or the thematic RDM under different semantic judgment tasks are illustrated (yellow: the left ATL; cyan: the left TPJ; red: the DMN sub-network; green: the PSN sub-network). The bars with solid
colors indicate taxonomic tasks. The bars with borders and dots indicate thematic tasks. ~: \( p < 0.1 \) or \( p < 0.05 \) (uncorrected). *: \( p < 0.05 \). (Bonferroni corrected, when a multiple comparison correction was needed).

Error bar: ± standard error.