



Dissociating the neural correlates of the sociality and plausibility effects in simple conceptual combination

Nan Lin^{1,2} · Yangwen Xu^{3,4} · Huichao Yang⁵ · Guangyao Zhang^{1,2} · Meimei Zhang¹ · Shaonan Wang^{6,7} · Huimin Hua^{1,2} · Xingshan Li^{1,2}

Received: 11 April 2019 / Accepted: 19 February 2020 / Published online: 5 March 2020
© Springer-Verlag GmbH Germany, part of Springer Nature 2020

Abstract

Neuroimaging studies have indicated that a brain network distributed in the supramodal cortical regions of the frontal, temporal, and parietal lobes plays a central role in conceptual processing. The activation of this network is modulated by two orthogonal dimensions in conceptual processing—the semantic features of individual concepts and the meaningfulness of conceptual combinations—but it remains unclear how the network is functionally organized along these two dimensions. In this fMRI study, we focused on two specific factors, i.e. the social semantic richness of words and the semantic plausibility of word combinations, along the two dimensions. In literature, the distributions of the effects of the two factors are very similar, but have not been rigorously compared in one study. We orthogonally manipulated the two factors in a phrase comprehension task and found a clear dissociation between their effects. The combination of these results with our previous findings reveals three adjacently distributed subnetworks of the supramodal semantic network, associated with the sociality effect, imageability effect, and semantic plausibility effect, respectively. Further analysis of the resting-state functional connectivity data indicated that the functional dissociation among the three subnetworks is associated with their underlying intrinsic connectivity structures.

Keywords Social concepts · Semantic plausibility · Semantics · Brain network · Phrase comprehension · Functional connectivity

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00429-020-02052-3>) contains supplementary material, which is available to authorized users.

✉ Nan Lin
linn@psych.ac.cn

- ¹ CAS Key Laboratory of Behavioral Science, Institute of Psychology, Beijing 100101, China
- ² Department of Psychology, University of Chinese Academy of Sciences, Beijing 100049, China
- ³ Center for Mind/Brain Sciences (CIMEC), University of Trento, 38123 Trento, Italy
- ⁴ International School for Advanced Studies (SISSA), 34136 Trieste, Italy
- ⁵ National Key Laboratory of Cognitive Neuroscience and Learning and IDG/McGovern Institute for Brain Research, Beijing Normal University, Beijing 100875, China
- ⁶ National Laboratory of Pattern Recognition, CASIA, Beijing 100190, China
- ⁷ University of Chinese Academy of Sciences, Beijing 100049, China

Introduction

Neuroimaging studies have indicated that a brain network consisting of supramodal cortical regions¹ plays a central role in conceptual processing (Binder et al. 2009; Ferstl et al. 2008). The network includes the angular gyrus (AG) and temporoparietal junctions (TPJ), dorsal and ventral medial prefrontal cortices (MPFC), posterior cingulate gyri (PC) and adjacent precuneus, fusiform gyrus and adjacent parahippocampus, middle temporal gyrus (MTG), and inferior frontal gyrus (IFG). Most of the semantic activations observed in neuroimaging studies are distributed within this supramodal cortical semantic network (Binder et al. 2009).

In addition to exhibiting a general preference to conceptual processes, the activation of the supramodal cortical semantic network is modulated by two orthogonal and broad dimensions in conceptual processing. The first dimension

¹ Supramodal cortical regions: cortical regions that receive multimodal input not dominated by any single modality (Binder and Desai 2011).

encompasses the semantic features of individual concepts. Current theories of concept representation generally assume that individual concepts are represented by sets of semantic features and there is considerable neuropsychological and neuroimaging evidence that the neural correlates of different types of semantic features, such as sensory, motor, and social semantic features, are at least partially dissociated from each other (Binder et al. 2016; Huth et al. 2016; Mahon and Caramazza 2009; Martin 2007). Consistent with this view, recent studies showed that the supramodal cortical semantic network contains fine-grained subdivisions whose activation is sensitive to different types of semantic features (Fernandino et al. 2016; Huth et al. 2016; Lin et al. 2018; Rice et al. 2018), indicating that the network contains subsystems to selectively process different types of semantic features (Fernandino et al. 2016; Lin et al. 2018). The second dimension is the meaningfulness of conceptual combinations. Several neuroimaging studies have employed the contrasts of high-versus low-meaningfulness conceptual combinations, such as plausible versus implausible word combinations (Forgács et al. 2012; Graves et al. 2010; Price et al. 2015), sentences versus word lists (Bonhage et al. 2014; Humphries et al. 2006; Lerner et al. 2011; Stowe et al. 1998; Vandenberghe et al. 2002; Xu et al. 2005), and coherent narratives versus unconnected sentences (Lerner et al. 2011; Xu et al. 2005), to investigate the neural correlates of combinatorial conceptual processes. Most of these studies found widespread activation within the supramodal cortical semantic network, indicating that the function of this network is not only limited to representing individual concepts but also includes the processing of global meanings of conceptual combinations.

Studies of conceptual processing often associate the effects of the two aforementioned dimensions with the two fundamental functions of conceptual processing: the effect of the semantic features of individual concepts is often associated with concept representation, and the meaningfulness effect of conceptual combinations is often associated with combinational conceptual processing. It remains controversial whether these two fundamental functions have common or separate neural correlates. Some researchers propose that a common brain network is ubiquitously involved in both functions (Blank et al. 2016). Others argue that there are separate neural correlates for the two functions but cannot reach a consensus on the specific structure–function correspondences (Hagoort 2013; Jung-Beeman 2005). Therefore, clarifying the cortical distributions of the effects of the two dimensions is important for revealing the functional organization of the supramodal cortical semantic network.

In this study, we focused on two specific factors, i.e., the social semantic richness (or “sociality,” see Lin et al. 2015, 2018) of words and the semantic plausibility of word combinations, along the two dimensions. The social semantic richness of a word refers to the extent to which the meaning

of a word is related to interpersonal interactions (Binder et al. 2016; Lin et al. 2018). Studies focused on the processing of words denoting high-sociality concepts such as human traits, human mental states, stereotypes, and social actions consistently found the activation of a set of brain regions, including the bilateral anterior temporal lobes (ATL), AG/TPJ, MPFC, and PC/precuneus (Contreras et al. 2012; Huth et al. 2016; Lin et al. 2015; Lin et al. 2018; Mitchell et al. 2002; Tamir et al. 2016; Wang et al. 2019; Zahn et al. 2007). These brain regions have strong intrinsic functional connectivity to each other and are largely dissociated from the brain regions that are involved in sensory–motor semantic processing (Lin et al. 2018). Therefore, it has been proposed that this set of brain regions constitutes a subsystem of the semantic network that selectively represents social semantic features of concepts (Binder et al. 2016; Huth et al. 2016).

The semantic plausibility of a word combination refers to the extent to which a word combination is meaningful (Price et al. 2015). Three previous fMRI studies have manipulated the semantic plausibility of word combinations and have observed the semantic plausibility effect (high plausibility > low plausibility) in the bilateral AG/TPJ, MPFC, PC/precuneus, and ATL (Forgács et al. 2012; Graves et al. 2010; Price et al. 2015). The semantic plausibility effect of word combinations is considered to reflect conceptual combination per se (Price et al. 2015) or the processes of relating combinational semantics to world knowledge (Pylkkänen et al. 2011).

We are interested in these two specific factors because, in the functional neuroimaging literature, the cortical distributions of their effects both involve the same set of broad brain regions, i.e., the AG/TPJ, the ATL, the MPFC, and the PC/precuneus. Two separate lines of studies have associated these brain regions to social concept representation (Binder et al. 2016; Huth et al. 2016) and combinational conceptual processing (Bemis and Pylkkänen 2011, 2013; Boylan et al. 2017; Graves et al. 2010; Price et al. 2015). We conducted a literature search to compare the previous neuroimaging findings on the two effects (see the Supplementary Materials for details). As shown in Fig. 1, the distributions of the activity peaks of the two effects have considerable similarity (see Tables S1 and S2 for details on the studies and activity peaks). The similarity between the neural correlates of the two effects implies two alternative theoretical possibilities. The first possibility is that the two effects are associated with two distinct sets of brain regions, whose distributions are close to but different from each other. In this case, distinguishing the distributions of the brain regions associated with the two effects would help to reveal the fine-grained functional organization of the supramodal cortical semantic network. The second possibility is that the brain areas related to the two effects are indeed highly overlapped. In this case, confirming the overlap between these brain regions would help to raise

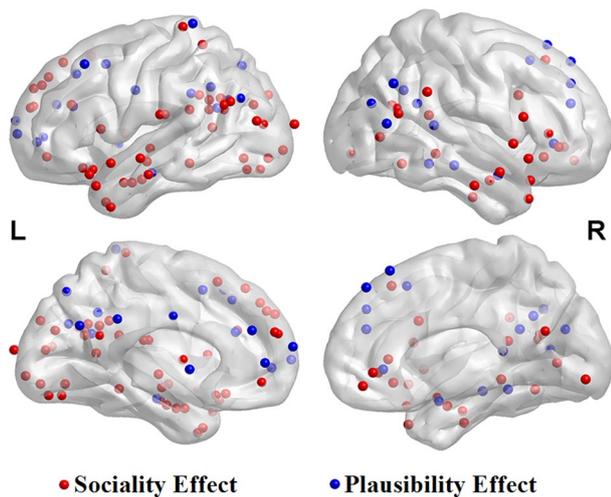


Fig. 1 Activity peaks reported in the previous studies on the sociality effect of words and the semantic plausibility effect of word combinations. See Tables S1 and S2 for the detailed activity peak coordinates and references

further theoretical questions: why do social concepts evoke stronger activation in the brain regions that support combinational conceptual processing than nonsocial concepts do? Is it because the comprehension of social concepts may evoke implicit combinational conceptual processing? One possible mechanism is that thinking of a social concept (e.g., steal) may evoke mentalizing processes that integrate the known facts about the concept (e.g., take a thing without the owner's consent) and the inferred mental states (e.g., to make a profit or to harm the owner) into a combinational representation (Leslie 1994). Because previous studies on the sociality and semantic plausibility effects varied in tasks, scanners, participants, stimuli, and analyzing methods (e.g., spatial normalization methods), it remains difficult to distinguish between the two aforementioned possibilities.

In this study, we rigorously compared the distributions of the sociality and semantic plausibility effects by orthogonally manipulating these two factors in a single fMRI experiment. In addition, we conducted further analysis of the resting-state functional connectivity (RSFC) to investigate whether the functional dissociation within the supramodal cortical semantic network revealed by the task fMRI data is associated with the underlying intrinsic connectivity structures.

Materials and methods

Participants

Twenty healthy undergraduate and graduate students (8 females) participated in the fMRI experiment. The mean

age of the participants was 22.5 years ($SD = 1.6$ years). All participants were right-handed and native Chinese speakers. None of the participants had suffered from psychiatric or neurological disorders or had ever sustained a head injury. All the protocols and procedures were approved by Institutional Review Board of the Magnetic Resonance Imaging Research Center of the Institute of Psychology of the Chinese Academy of Sciences, and each participant read and signed an informed consent form before the experiment.

Design and materials

The stimuli are all Chinese verb-noun phrases, each of which consists of a two-character verb and a two-character noun. The social semantic richness of the component words and the plausibility of the phrases were manipulated. Therefore, the experiment contained four conditions, namely, the high-sociality and high-plausibility condition (HSHP; e.g., 关押犯人, meaning “to detain suspects”), the high-sociality and low-plausibility condition (HSLP; e.g., 关押贺卡, meaning “to detain greeting cards”), the low-sociality and high-plausibility condition (LSHP; e.g., 打磨刀具, meaning “to sharpen a knife”), and the low-sociality and low-plausibility condition (LSLP; e.g., 打磨棉花, meaning “to sharpen cotton”).

The component words of the stimuli were chosen from 275 verbs and 275 nouns. Two prior rating experiments were conducted with 16 additional participants to obtain the sociality and imageability ratings for these words. The imageability was chosen as a control variable, as its effect on brain activation overlaps with that of sociality (Lin et al., 2018). In the sociality rating experiment, participants were asked to classify the words according to how often the meaning of a word involves an interaction between people (5 = always, 4 = typically, 3 = sometimes, 2 = rarely, and 1 = never). In the imageability rating experiment, participants were asked to rate the extent to which the meaning of a word recalls an image (5 = very high and 1 = very low). In both rating experiments, high inter-rater reliability (Shrout and Fleiss 1979) was shown by the intraclass correlation coefficients (ICC; sociality rating: $ICC [2, 16] = 0.955$, imageability rating: $ICC [2, 16] = 0.958$).

Based on the results of these rating experiments, we selected 120 high-sociality words (60 verbs and 60 nouns) to form the high-sociality (HSHP and HSLP) phrases and 120 low-sociality words (60 verbs and 60 nouns) to form the low-sociality (LSHP and LSLP) phrases. The sociality ratings (see Table 1) were significantly different between the high- and low-sociality verbs ($t [118] = 25.351$; $p < 0.001$) and between the high- and low-sociality nouns ($t [118] = 32.310$; $p < 0.001$). The imageability ratings and the log word frequencies obtained from the

Chinese Linguistic Data Consortium (2003) corpus (see Table 1) were matched between the high- and low-sociality verbs and between the high- and low-sociality nouns (ts [118] < 1).

The selected words were used to form 240 phrases (60 per condition; see Table S3 for the full version of the 240 phrases). Each word appeared twice in the experiment, once in a high-plausibility and once in a low-plausibility phrase. Therefore, the component words were identical between the HSHP and HSLP conditions and between the LSHP and LSLP conditions. The plausibility manipulation was confirmed by an independent rating experiment with 16 additional participants, in which participants were asked to rate the extent to which a phrase is semantically plausible (5 = very high and 1 = very low; see Table 1). The inter-rater reliability of the plausibility rating experiment was very high (ICC [2, 16] = 0.944). The plausibility ratings were significantly different between the high-plausibility and low-plausibility conditions (ts [118] > 64.322; ps < 0.001) and were matched between the HSHP and LSHP conditions and between the HSLP and LSLP conditions (ts [118] < 1). We also obtained the co-occurrence frequency of the component words of each stimulus in a corpus of materials from the Giganews (<https://cn.giganews.com/>) and Baidu Baike (<https://baike.baidu.com/>) websites, containing two billion words. Following Price et al. (2015), we took the $\log(x + 1)$ of this co-occurrence frequency and referred to this measure as the “combinatorial strength” of the component words. Replicating the findings of Price et al. (2015), the ratings of the phrases’ plausibility and the combinatorial strength of the component words were strongly correlated with each other (Spearman’s $\rho = 0.816$; $p < 0.001$). The combinatorial strength (see Table 1) was significantly different between the high-plausibility and low-plausibility conditions (ts [118] > 11.542; ps < 0.001) and was not different between the HSHP and LSHP conditions (t [118] < 1) or between the HSLP and LSLP conditions (t [118] = 1.487; $p = 0.140$).

Procedures

The fMRI experiment employed an event-related design, containing four runs of six minutes and 10 s each. Each run included 60 trials (15 for each condition). In the first 10 s of each run, participants were shown a fixation. Then, they performed a phrase comprehension task in which they saw a Chinese verb–noun phrase and were asked to indicate whether the phrase was semantically plausible by pressing buttons. In each trial, the phrase appeared for 3 s, followed by a jitter fixation of at least 1 s. The length of the jitter fixations and the order of the trials were optimized using

Table 1 Lexical–semantic variables for each condition

Condition	Example	Number of characters/syllables	Semantic plausibility	Combinatorial strength	Sociality		Imageability		Log Word Frequency	
					Verb component	Noun component	Verb component	Noun component	Verb component	Noun component
HSHP	关押犯人 (to detain suspects)	4 ± 0	4.81 ± 0.27	1.4 ± 0.86	4.18 ± 0.54	4.29 ± 0.49	3.38 ± 0.79	4.96 ± 1.01	0.85 ± 0.34	1.01 ± 0.45
HSLP	关押贺卡 (to detain greeting cards)	4 ± 0	1.22 ± 0.31	0.02 ± 0.11	4.18 ± 0.54	4.29 ± 0.49	3.38 ± 0.79	4.96 ± 1.01	0.85 ± 0.34	1.01 ± 0.45
LSHP	打磨刀具 (to sharpen a knife)	4 ± 0	4.77 ± 0.29	1.42 ± 0.82	2.03 ± 0.37	1.66 ± 0.40	3.47 ± 0.99	5.07 ± 1.75	0.83 ± 0.41	1.04 ± 0.48
LSLP	打磨棉花 (to sharpen cotton)	4 ± 0	1.22 ± 0.27	0.07 ± 0.23	2.03 ± 0.37	1.66 ± 0.40	3.47 ± 0.99	5.07 ± 1.75	0.83 ± 0.41	1.04 ± 0.48

The lexical–semantic variables are presented in the form of mean ± standard deviation. The “combinatorial strength” is the $\log(x + 1)$ of the co-occurrence frequency of the two component words in a corpus of two billion words combining materials from Giganews (<https://cn.giganews.com/>) and Baidu Baike (<https://baike.baidu.com/>). The log word frequency is the logarithm of the word frequency (per million) in the Chinese Linguistic Data Consortium (2003) corpus

optseq2 (<https://surfer.nmr.mgh.harvard.edu/optseq/>) and were counterbalanced across runs and participants.

Image acquisition and preprocessing

The MRI data were collected using a GE Discovery MR750 3 T scanner at the Magnetic Resonance Imaging Research Center of the Institute of Psychology of the Chinese Academy of Sciences. T1-weighted structural images were obtained using a spoiled gradient-recalled pulse sequence in 176 sagittal slices with 1.0-mm isotropic voxels. Functional blood-oxygenation-level-dependent data were collected using a gradient-echo echo-planar imaging sequence in 42 near-axial slices with 3.0-mm isotropic voxels (matrix size = 64 × 64; repetition time = 2000 ms; echo time = 30 ms). Before the tasks were performed, resting-state fMRI data were collected with a single run lasting 8 min, obtained in 33 axial slices with 3.4 mm × 3.4 mm × 4 mm voxels (matrix size = 64 × 64; repetition time = 2000 ms; echo time = 30 ms).

The fMRI data were preprocessed using the Statistical Parametric Mapping software (SPM8; <https://www.fil.ion.ucl.ac.uk/spm/>). For the preprocessing of the task fMRI data, the first five volumes of each functional run were discarded to reach signal equilibrium. Slice timing and 3-D head motion correction were performed. After that, a mean functional image was obtained for each participant, and the structural image of each participant was coregistered to the mean functional image. Then, the structural image was segmented using the unified segmentation module (Ashburner and Friston 2005). The parameters obtained during segmentation were used to normalize the functional images of each participant into the Montreal Neurological Institute space. Then, functional images were spatially smoothed using a 6-mm full-width-half-maximum Gaussian kernel.

When preprocessing the resting-state fMRI data, the first ten volumes were discarded, followed by steps that were similar to those of the task fMRI data, except that the effects of nuisance variables, including 6 rigid head motion parameters, white matter signal, and cerebrospinal fluid signal, were regressed from the functional images before spatial normalization. After those steps, linear trends were removed, and the images were 0.01–0.1 Hz band-pass filtered to reduce the effects of low-frequency drifts and high-frequency noise.

Data analysis

Statistical analysis was performed using 2-level mixed-effects models implemented in SPM8. At the first level, a general linear model was applied to examine the fixed effect of each participant. The four conditions (HSHP, HSLP, LSHP, and LSLP) were set as covariates of interest. Each trial was modeled as an event with a duration of 0 s. Six head

motion parameters obtained by the head motion correction were included as nuisance regressors. The effect of response time (RT) was also included as a nuisance covariate (Yarkoni et al. 2009). A high-pass filter (128 s) was used to remove low-frequency signal drift.

The participant-specific statistical maps obtained in the first-level analysis were then entered into a second-level random-effect analysis. A flexible factorial design was applied to accommodate a 2 × 2 within-subject design. The main effects, that is, those of sociality and plausibility, and their interaction were examined. The false-positive rate was controlled at $\alpha < 0.05$ using cluster-level FWE correction as implemented in SPM8 (voxel-wise $p < 0.001$). The results were visualized using the BrainNet Viewer software (Xia et al. 2013).

To examine whether there is dissociation between the neural correlates of the sociality and semantic plausibility effects, we conducted two analyses. In the first analysis, we examined whether the brain regions showing the sociality effect and those showing the plausibility effect in the whole brain analysis overlapped each other. In the second analysis, to enhance the statistical power, we used a region-of-interest (ROI)-based approach in which the beta estimates of all voxels were averaged within each ROI. We defined the brain regions showing sociality and plausibility effects in the whole brain analysis as ROIs, and examined whether any of the sociality ROIs showed a plausibility effect or vice versa.

Since the sociality effect observed in the present study was much less extensive than that observed in previous studies (e.g., Lin et al. 2015; Lin et al. 2018), possibly because of the relatively shallow semantic processing and low effort required by the task in the present study (Meyer et al. 2012, 2015), we conducted two supplementary analyses based on the results of a recent study (Lin et al. 2018), which identified all the classic regions of the social semantic network. Lin et al. (2018) used the same MRI scanner, experimental parameters (number of conditions, number of items, length of trials, length of jitter fixations, number and length of runs), and data analyzing procedures used in the present study. Therefore, the data of the two studies are highly comparable. The only differences between the two studies are in the participants, stimuli (two verbs per trial vs. a verb–noun phrase per trial), and task requirements (semantic relatedness judgment vs. plausibility judgment). In the first analysis, we examined whether the sociality clusters of Lin et al. (2018) overlapped with the plausibility clusters of the present study. In the second analysis, we defined the sociality clusters of Lin et al. (2018) as ROIs and examined whether any of these ROIs showed a significant plausibility effect in the present study.

As shown in “Results” section, all such analyses indicated that the brain regions associated with the sociality and semantic plausibility effects are largely dissociated from

each other. We thus conducted two follow-up analyses to investigate whether the dissociation between the two sets of brain regions is associated with their intrinsic functional connectivities. In the first analysis, we examined whether the dissociation between sociality and plausibility effects follows the divides of the seven large-scale intrinsic brain networks identified by Yeo et al. (2011), obtained based on the RSFC data of 1000 healthy participants. Overlapping our results with the seven networks can indicate to what extent the large-scale intrinsic connectivity structures of the human brain may constrain the dissociation between the two effects. For each cluster showing a sociality or plausibility effect in the present study, we calculated the number of voxels overlapping the seven intrinsic brain networks (Yeo et al. 2011). The overall distributions of the two effects in the seven intrinsic brain networks were also calculated and compared to each other.

In the second analysis, we defined the clusters showing the sociality and plausibility effects in the present study as ROIs, and calculated the RSFC between each pair of ROIs. To examine whether the dissociation between the two sets of ROIs (sociality ROIs and plausibility ROIs) is associated with their intrinsic functional connectivity properties, we compared the average RSFC within each set of ROIs to the average RSFC across the two different sets of ROIs. If the two sets of ROIs correspond to two intrinsic brain networks, we would expect the average RSFC within each set of ROIs to be stronger than that across the two sets. The analysis was conducted using the Resting state fMRI Data Analysis Toolkit (REST version 1.8; <https://www.restfmri.net>) (Song et al. 2011). For each participant, the ROI-to-ROI RSFC was represented by the correlation coefficient between the mean time series of each pair of ROIs. The statistical analysis was performed using within-subject *t* tests, after the correlation coefficients were Fisher-transformed to improve normality (Silver and Dunlap 1987). For visualization purposes, we also created a matrix in which the correlation coefficient between each pair of ROIs was Fisher-transformed and averaged across subjects, and then inverse-Fisher-transformed for presentation. Moreover, as in the analysis of brain activation, we conducted a supplementary ROI-based RSFC analysis using the sociality clusters of Lin et al. (2018) and the plausibility clusters of the present study as ROIs.

Beyond the main question of the present study, i.e., whether the brain network supporting social semantic processing and that supporting semantic plausibility judgment are dissociated from each other, a further important question is whether these two networks are dissociated from the other semantic subnetworks, such as the sensory–motor semantic network. By comparing the sociality and imageability effects during word comprehension, Lin et al. (2018) revealed that the social and- sensory–motor semantic networks are adjacently distributed and largely dissociated from each other.

Therefore, to reveal the functional subdivisions within the semantic system more comprehensively, we conducted supplementary analyses to compare the sensory–motor semantic network revealed by Lin et al. (2018) (as reflected by the imageability effect) and the network supporting semantic plausibility judgment revealed by the present study, in terms of their distributions and functional connectivity properties.

Results

Behavioral results

The participants were asked to judge the plausibility of phrases by pressing buttons in the fMRI scanner. The mean RTs of the HSHP, HSLP, LSHP, and LSLP conditions were 1184 ms (SD = 183 ms), 1359 ms (SD = 231 ms), 1195 ms (SD = 206 ms), and 1307 ms (SD = 209 ms), respectively. The main effect of plausibility on RTs was statistically significant ($F [1, 19] = 21.578, p < 0.001$, low plausibility > high plausibility), while the main effect of sociality and the interaction effect between sociality and plausibility were not (sociality: $F [1, 19] = 3.062, p = 0.096$; interaction: $F [1, 19] = 3.753, p = 0.068$). Meanwhile, the mean semantic plausibility ratings (plausible = 1, implausible = 0) of the HSHP, HSLP, LSHP, and LSLP conditions were 0.97 (SD = 0.03), 0.05 (SD = 0.04), 0.96 (SD = 0.03), and 0.06 (SD = 0.05), respectively. The main effect of plausibility on the ratings was statistically significant ($F [1, 19] = 7078, p < 0.001$, high plausibility > low plausibility), and the main effect of sociality and the interaction effect between sociality and plausibility were not (sociality: $F [1, 19] < 1$; interaction: $F [1, 19] = 1.508, p = 0.234$).

fMRI results

Results of the whole brain analysis

The results of the whole brain analysis of the fMRI data are shown in Table 2. The left ATL (and a small number of voxels of the left IFG) and the left MTG/AG showed the sociality effect (high > low) and no region showed the reverse pattern (Fig. 2a). The right supramarginal gyrus (SMG), left inferior parietal lobe (IPL), MPFC, anterior cingulate gyri, median cingulate and paracingulate gyri, and right superior and middle frontal gyri showed the semantic plausibility effect (high > low), while the left precentral gyrus, supplementary motor area (SMA), and IFG showed the reverse plausibility effect (high < low; Fig. 2b). No significant interaction effect between sociality and plausibility was detected.

We compared the distributions of the brain regions showing sociality and plausibility effects. The sociality and plausibility clusters we found did not overlap with each other

Table 2 Results of the whole brain analysis (voxel-wise $p < 0.001$, cluster-wise FWE $p < 0.05$)

Contrast	Anatomical region of the peak voxel	Cluster size (voxels)	MNI coordinates of peak voxel (x, y, z)			Peak t value
Main effect of sociality						
HS > LS	Left middle temporal gyrus	204	-57	-3	-18	9.110
	Left angular gyrus	147	-42	-63	24	6.249
HS < LS	None					
Main effect of plausibility						
HP > LP	Right supramarginal gyrus	183	54	-45	42	6.675
	Left inferior parietal lobe	193	-54	-51	39	6.217
	Right median cingulate and paracingulate gyri	131	3	-30	42	6.005
	Right medial superior frontal gyrus	420	9	51	6	5.634
	Right dorsolateral superior frontal gyrus	67	15	54	30	5.124
	Right middle frontal gyrus	69	36	21	51	4.624
	Right middle frontal gyrus, orbital part	49	39	54	-3	4.197
HP < LP	Left precentral gyrus	133	-36	-15	60	-5.625
	Left supplementary motor area	83	-3	-6	57	-5.177
	Left inferior frontal gyrus, triangular part	100	-54	24	9	-4.636
“Sociality × Plausibility” interaction	None					

The anatomical regions of the peak voxels were identified using the automated anatomical labeling template (Tzourio-Mazoyer et al. 2002)

(Fig. 2c). The closest sociality and plausibility clusters are located in the left MTG/AG (sociality) and dorsal IPL (plausibility) respectively, whose peaks are 22.6 mm away from each other. As the sociality effect observed in the present study was much less extensive than that observed in the previous studies, we further investigated whether the plausibility effect we observed overlapped with the sociality effect observed in a previous study (Lin et al. 2018). As shown in Fig. 2d, the two sets of brain regions were basically dissociated from each other, and only three very small overlaps were found (11, 3, and 2 voxels, respectively). In addition, the overlaps between the plausibility effect we observed in the present study and the imageability effect observed by Lin et al. (2018) are also very small (Fig. 2d).

The observed plausibility effect in this study largely replicated the findings of previous studies that used the same or similar tasks (Forgács et al. 2012; Graves et al. 2010; Price et al. 2015). However, using the plausibility judgment task to investigate the semantic plausibility effect carries the risk of confounding the semantic plausibility effect with the effect of the task goal. To address this issue, we defined the plausibility clusters of the present study as ROIs and conducted a supplemental ROI analysis on the data from a previous study (Lin et al. 2016), whose design can partially tease apart the effect of combinational conceptual processing from the effect of goal-directed cognition. The full details of this supplementary analysis are given in the Supplementary Materials. To summarize the main finding, among the seven ROIs, six of them showed

the predicted data pattern according to the meaningfulness of conceptual combinations, which is largely consistent with the semantic plausibility effect observed in our study. In the two ROIs where we observed the strongest plausibility effects in our study, i.e., the clusters located in the right SMG and the left IPL, the activation patterns of Lin et al. (2016) can be explained by the meaningfulness of conceptual combinations but not by the task goal, thus supporting the hypothesis that these areas are involved in combinational conceptual processing. In the other ROIs, the activation patterns of Lin et al. (2016) cannot clearly tease apart the effect of combinational conceptual processing from the effect of goal-directed cognition; thus, the plausibility effect observed in these areas should be explained with greater caution.

Results of the ROI analysis

None of the sociality clusters of the present study or those of Lin et al. (2018) showed a significant plausibility effect, and none of the plausibility clusters of the present study showed a significant sociality effect (see Table 3 for the detailed statistical results). Among the six sociality clusters of Lin et al. (2018), only three clusters (left ATL, right ATL, and left MTG) showed a significant sociality effect (high > low; see Table 3) in the present study, indicating that the involvement of the other brain regions of the social semantic network might be modulated not only

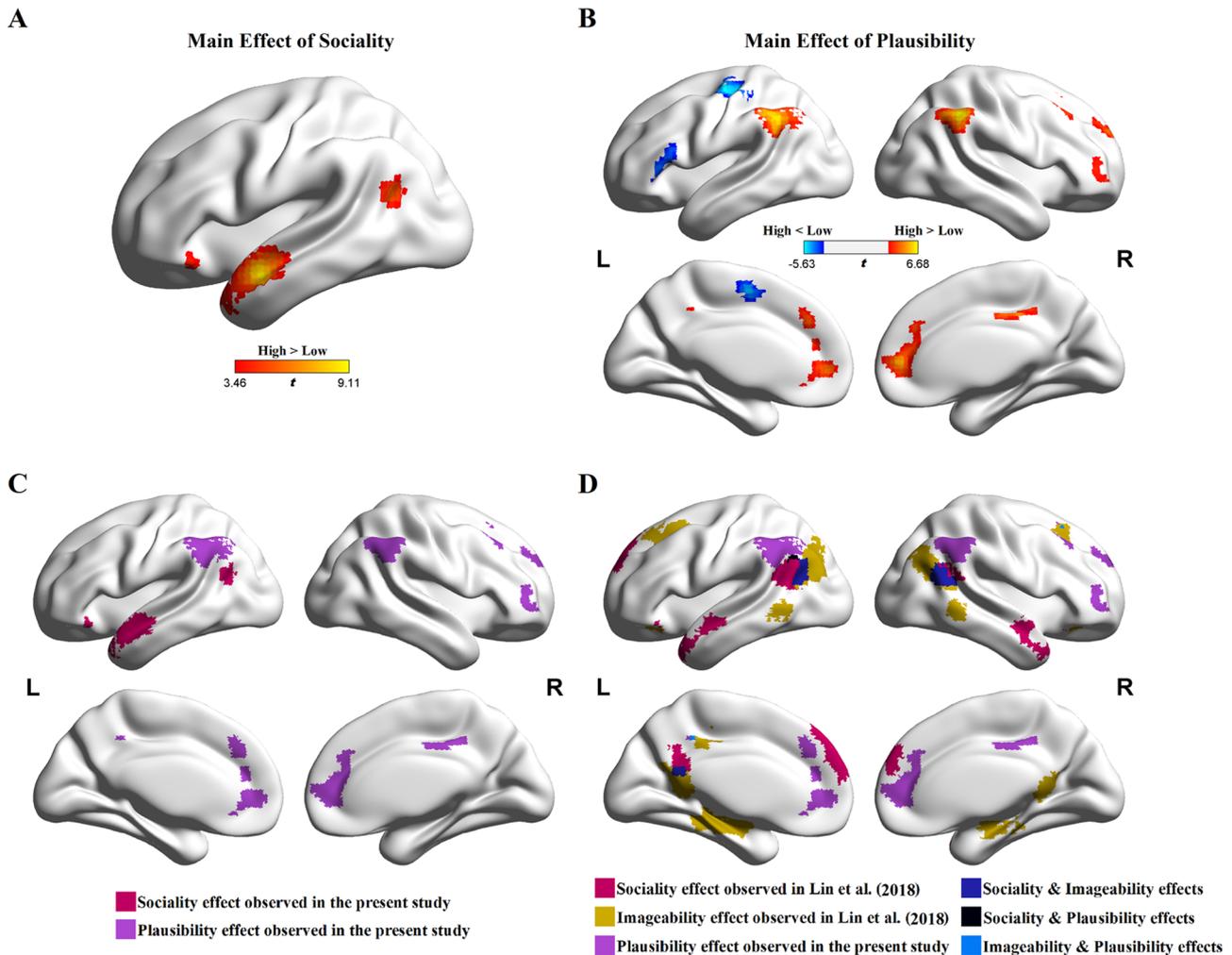


Fig. 2 The sociality and plausibility effects obtained in the whole brain analysis. **a** The main effect of sociality, **b** the main effect of plausibility, **c** the dissociation between the sociality and plausibility effects observed in the present study, **d** the dissociation and overlap between the plausibility effect observed in the present study and

the sociality and imageability effects observed in Lin et al. (2018). For the results of the whole brain analysis (**a**, **b**), the false-positive rate was controlled at $\alpha < 0.05$ using cluster-level FWE correction as implemented in SPM8 (voxel-wise $p < 0.001$)

by the social semantic richness of stimuli but also by other factors, such as task requirements.

Overlapping the sociality and plausibility clusters with the large-scale intrinsic brain networks

To examine whether the dissociation between the sociality and plausibility effects follows the divides of the intrinsic large-scale brain networks, we examined the distributions of the sociality and plausibility clusters in the seven intrinsic large-scale networks proposed by Yeo et al. (2011), which were labeled as visual, somatomotor, dorsal attention, ventral attention, limbic, frontoparietal, and default networks. For each cluster showing the sociality or plausibility effect in the present study, the number of

its voxels overlapping the templates of the seven intrinsic brain networks was calculated (Table 4). The sociality clusters mainly overlap with the default network, and their overlaps with the other networks are small. The plausibility clusters mainly overlap with the default and frontoparietal control networks, and their overlaps with the other networks are small. All of the seven plausibility clusters overlap the frontoparietal control network, and six of them overlap the default network. Therefore, the result shows a systematic difference between the distributions of sociality and plausibility effects across the seven large-scale brain networks. The sociality clusters are mainly localized within the default network, while the plausibility clusters overlap with both the default network and the frontoparietal control network (Figure S1).

Table 3 Statistical results of the ROI analysis

ROI	Beta (mean ± standard deviation)				Main effect of sociality		Main effect of plausibility		“Sociality × Plausibility” interaction	
	HSHP	HSLP	LSHP	LSLP	F	p	F	p	F	p
Sociality clusters of the present study										
Left middle temporal gyrus	2.16 ± 2.08	2.38 ± 2.96	0.22 ± 2.29	0.23 ± 2.24	–	–	0.171	0.684	–	–
Left angular gyrus	0.22 ± 3.14	0.16 ± 3.7	–1.98 ± 3.02	–1.98 ± 2.91	–	–	0.004	0.9	–	–
Plausibility clusters of the present study										
Right supramarginal gyrus	–0.75 ± 3.46	–3.66 ± 2.67	–0.5 ± 3.64	–3.25 ± 3.32	0.777	0.389	–	–	–	–
Left inferior parietal lobe	–1.61 ± 3.07	–4.63 ± 2.22	–1.64 ± 3.15	–3.73 ± 3.05	1.914	0.183	–	–	–	–
Right median cingulate and paracingulate gyri	–1.89 ± 3.35	–4.5 ± 3.04	–1.41 ± 2.72	–3.7 ± 2.71	3.335	0.084	–	–	–	–
Right medial superior frontal gyrus	–1.21 ± 2.65	–3.77 ± 3.35	–0.52 ± 2.72	–2.85 ± 2.64	4.680	0.043	–	–	–	–
Right dorsolateral superior frontal gyrus	–1.24 ± 3.04	–3.81 ± 3.82	–1.1 ± 3.4	–3.01 ± 3.47	1.274	0.273	–	–	–	–
Right middle frontal gyrus	–1.61 ± 3.31	–3.5 ± 2.53	–0.97 ± 3.06	–3.06 ± 3.15	2.860	0.107	–	–	–	–
Right middle frontal gyrus, orbital part	0.5 ± 5.32	–2.24 ± 3.85	0.3 ± 4.78	–2.18 ± 4.71	0.022	0.883	–	–	–	–
Sociality clusters of Lin et al. (2018)										
Left anterior temporal lobe	1.89 ± 2.38	2.18 ± 3.12	0.04 ± 2.51	0.25 ± 2.23	34.466	0.000	0.820	0.376	0.012	0.913
Left superior frontal gyrus	0.26 ± 3.20	–0.10 ± 3.51	–0.41 ± 3.22	–1.10 ± 2.75	3.858	0.064	1.163	0.294	0.199	0.661
Left middle temporal gyrus	–0.87 ± 3.16	–1.68 ± 3.53	–2.56 ± 2.64	–3.00 ± 3.02	15.447	0.001	2.307	0.145	0.248	0.625
Right anterior temporal lobe	0.94 ± 2.00	0.58 ± 2.58	–0.19 ± 2.18	–0.27 ± 2.27	8.926	0.008	0.620	0.441	0.266	0.612
Right superior temporal gyrus	–1.94 ± 3.01	–3.03 ± 2.72	–2.50 ± 2.49	–2.85 ± 2.39	0.287	0.598	3.278	0.086	1.680	0.210
Left posterior cingulate gyrus	–2.11 ± 3.20	–3.23 ± 2.79	–3.03 ± 2.91	–4.09 ± 3.37	3.304	0.085	2.870	0.107	0.009	0.924

To avoid the double dipping problem, the cells in which the definition of the ROI is not independent of the statistical test are labeled as “–”

None of the sociality ROIs showed a significant plausibility effect or vice versa. A plausibility ROI located in the right medial superior frontal gyrus even showed a reverse sociality effect (high < low; uncorrected)

Table 4 The distributions of sociality and plausibility effects in the seven intrinsic large-scale brain networks (Yeo et al. 2011)

Contrast	Anatomical region of the peak voxel	The percentage of voxels in a cluster (the number of voxels) overlapping with the seven large-scale intrinsic brain networks							
		Visual	Somatomotor	Dorsal attention	Ventral attention	Limbic	Frontoparietal	Default	Outside the seven networks
The sociality effect (high > low)	Left middle temporal gyrus	0% (0)	0% (0)	7% (10)	0% (0)	0% (0)	0% (0)	68% (100)	25% (37)
	Left angular gyrus	0% (0)	3% (6)	0% (0)	0% (0)	4% (9)	0% (0)	90% (183)	3% (6)
	Total	0% (0)	2% (6)	3% (10)	0% (0)	3% (9)	0% (0)	81% (283)	12% (43)
The plausibility effect (high > low)	Right supramarginal gyrus	0% (0)	0% (0)	6% (11)	13% (26)	0% (0)	28% (54)	47% (91)	6% (11)
	Left inferior parietal lobe	0% (0)	0% (0)	0% (0)	1% (1)	0% (0)	61% (112)	38% (69)	1% (1)
	Right median cingulate and paracingulate gyri	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	98% (48)	0% (0)	2% (1)
	Right medial superior frontal gyrus	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	61% (42)	35% (24)	4% (3)
	Right dorsolateral superior frontal gyrus	0% (0)	0% (0)	0% (0)	9% (6)	0% (0)	16% (11)	63% (42)	12% (8)
	Right middle frontal gyrus	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	8% (32)	85% (357)	7% (31)
	Right middle frontal gyrus, orbital part	0% (0)	6% (8)	1% (1)	27% (36)	0% (0)	28% (37)	30% (39)	8% (10)
	Total	0% (0)	1% (8)	1% (12)	6% (69)	0% (0)	30% (336)	56% (622)	6% (65)

Results of the ROI-based RSFC analysis

To further investigate whether the dissociation between the sociality and plausibility clusters of the present study can be revealed by the RSFC data, we compared the average RSFC within each type of clusters (sociality or plausibility) with the average RSFC across the two types. We found that the average RSFC within our sociality and plausibility clusters were both significantly stronger than the average RSFC across the two types of clusters (mean Fisher-transformed correlation [SD]: within sociality clusters = 0.81 [0.29]; within plausibility clusters = 0.43 [0.14]; across sets = 0.22 [0.14]; $t_s [19] > 5.70$, $p < 0.001$; see Fig. 3 for the average ROI-to-ROI RSFC matrix across participants), indicating that the dissociation between the two types of clusters is associated with their intrinsic functional connectivities.

Since the comparison between the plausibility clusters of the present study and the sociality and imageability clusters of Lin et al. (2018) revealed dissociations between the three semantic subnetworks (Fig. 2d), we conducted a further ROI-based RSFC analysis to investigate whether such dissociations can be revealed by the RSFC data. We found

that the average RSFC within the sociality clusters of Lin et al. (2018) and within the plausibility clusters of the present study were both significantly stronger than the average RSFC across them (mean Fisher-transformed correlation [SD]: within sociality clusters = 0.80 [0.17]; within plausibility clusters = 0.43 [0.14]; across sets = 0.29 [0.13]; $t_s [19] > 4.44$, $p < 0.001$; see Figure S2 for the average ROI-to-ROI RSFC matrix across participants). The average RSFC within the imageability clusters of Lin et al. (2018) and that within the plausibility clusters of the present study were both significantly stronger than the average RSFC across them (mean Fisher-transformed correlation [SD]: within sociality clusters = 0.44 [0.12]; within plausibility clusters = 0.43 [0.14]; across sets = 0.30 [0.13]; $t_s [19] > 5.78$, $p < 0.001$; see Figure S3 for the average ROI-to-ROI RSFC matrix across participants). Therefore, the dissociation between the plausibility clusters and the other two types of clusters appears to be associated with their intrinsic functional connectivities. Replicating the finding of Lin et al. (2018), the average RSFC within the sociality clusters of Lin et al. (2018), but not that within the imageability clusters of Lin et al. (2018), was significantly stronger than the average RSFC across the

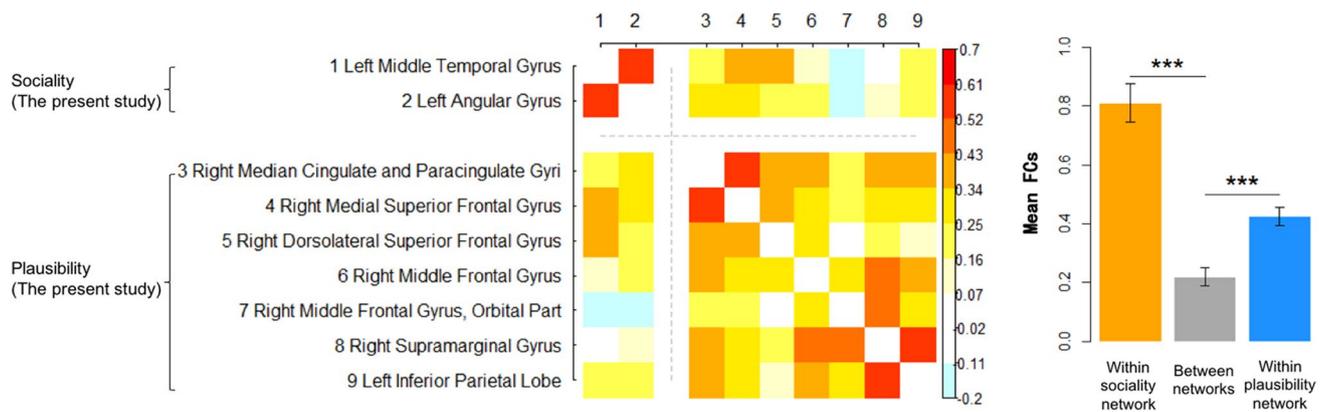


Fig. 3 The matrix of ROI-to-ROI RSFC in which the ROIs were the clusters showing sociality and plausibility effects in the whole brain analysis. The matrix shows the average RSFC between each pair of ROIs across participants

sociality and imageability clusters (mean Fisher-transformed correlation [SD]: within sociality clusters = 0.80 [0.17]; within imageability clusters = 0.44 [0.12]; across sets = 0.45 [0.13]; within sociality network vs. between networks: t [19] = 10.37, $p < 0.001$; within imageability network vs. between networks: t [19] = 1.1, $p = 0.285$; see Figure S4 for the average ROI-to-ROI RSFC matrix across participants), indicating that the dissociation between these two types of clusters is partially associated with their intrinsic functional connectivities.

Discussion

We investigated the neural correlates of the sociality and plausibility effects in simple conceptual combination using a phrase comprehension task. The social semantic richness of the component words of the phrases modulated the activation of the left ATL and MTG/AG, with the high-sociality words evoking higher activation than the low-sociality words. The semantic plausibility of the phrases modulated the activation of several brain regions: the bilateral dorsal IPL, MPFC, anterior cingulate gyri, median cingulate and paracingulate gyri, and right superior and middle frontal gyri showed higher activation to plausible phrases than implausible ones, while the left precentral gyrus, SMA, and IFG showed the reverse pattern. The effects of sociality and semantic plausibility showed no overlap or interaction with each other in the whole brain analysis. The sociality cluster in the left MTG/AG and the plausibility cluster in the left dorsal IPL are relatively close to each other, but still with a distance of 22.6 mm between their foci. In a further ROI analysis, no ROI defined by the sociality clusters of the whole brain analysis showed a significant plausibility effect or vice versa, indicating that the clusters that are sensitive to one of the two factors are relatively insensitive

to the other. These findings indicate that the brain network supporting social semantic processing and that supporting semantic plausibility judgment are largely dissociated from each other.

We further compared the results of the present study with those of Lin et al. (2018). We defined the sociality clusters observed by Lin et al. (2018) as ROIs and found that none of them showed a significant plausibility effect in the present study. In addition, the sociality and imageability clusters observed by Lin et al. (2018) are both largely dissociated from the plausibility clusters of the present study. Therefore, the combination of our present results and the findings of Lin et al. (2018) reveals three adjacently distributed brain networks within the semantic system, which are associated with social semantic processing (as reflected by the sociality effect), sensory–motor semantic processing (as reflected by the imageability effect), and semantic plausibility judgment (as reflected by the plausibility effect), respectively. The three networks are largely dissociated from each other, with fine-grained subdivisions located in the bilateral temporo-parieto-occipital junctions, MPFC, and PC/precuneus (Fig. 2d).

We conducted two further analyses to examine whether the dissociation between the brain networks in our task fMRI experiment is associated with their intrinsic functional connectivities. In the first analysis, we found a systematic difference between the sociality and plausibility clusters obtained in the present study in terms of their distribution across the seven intrinsic large-scale networks proposed by Yeo et al. (2011): the sociality effect was mainly located within the default network, while the plausibility effect overlaps with both the default network and the frontoparietal control network. In the second analysis, we found that the RSFC within the sociality and plausibility clusters were both significantly stronger than the RSFC across the two groups of clusters, indicating that the dissociation between the two groups of

clusters is associated with their intrinsic functional connectivities. In addition, similar RSFC dissociation patterns were also found between the plausibility clusters obtained in the present study and the sociality and imageability clusters obtained in Lin et al. (2018), indicating that the functional dissociations between the neural correlates of the three aspects of conceptual processing are related to their intrinsic functional connectivities.

The cortical distributions of the three semantic subnetworks identified in the present study and by Lin et al. (2018) largely converge with the findings of a recent parcellation study (Xu et al. 2016), in which the supramodal cortical semantic network identified by Binder et al. (2009) was dissociated into three subnetworks using a data-driven approach based on RSFC data. In particular, both Xu et al. (2016) and our task fMRI studies dissociated the temporo-parieto-occipital junction into three subdivisions, respectively, located in the anterior dorsal, anterior ventral, and posterior parts. Therefore, the convergent findings from the present study provide important insight about the cognitive functions of the subnetworks obtained by Xu et al. (2016).

The sociality effect observed in the present study was much less extensive than that observed in previous studies of social semantic processing (e.g., Lin et al. 2015; Lin et al. 2018). The right MTG/AG, MPFC, and PC/precuneus, which showed a strong sociality effect in previous studies, did not show such effect in this study. This finding is interesting, but the underlying reason still requires further investigation. Because the plausibility judgment task used in the present study revealed much shorter RT (approximately 260–320 ms faster) than the relatedness judgment task used in the previous studies (Lin et al. 2015, 2018), we infer that the lack of social semantic activation in the right MTG/AG, MPFC, and PC/precuneus may be related to relatively shallow semantic processing and low cognitive effort required by the plausibility judgment task. Consistent with this view, recent neuroimaging studies have showed that when processing social conceptual information the activation of the MPFC, PC, and TPJ is strongly modulated by the effort required by the task (Meyer et al. 2012, 2015).

It should be noted that although studies on conceptual processing often associate the effect of social semantic richness with the function of social concept representation (Huth et al. 2016; Tamir et al. 2016), the brain regions showing the sociality effect have also been associated with two other related functions. The first function is called theory of mind (ToM), which refers to the ability to understand the mental states of others (Gallagher et al. 2000; Saxe and Kanwisher 2003; Schurz et al. 2014). Lin et al. (2018) found that the brain areas showing the sociality effect in a semantic comprehension task largely overlap with those involved in a ToM task. This overlap can be easily explained with social concept representation because ToM studies typically

use high-sociality stimuli (e.g., stories about peoples' false-beliefs) as the target stimuli and low-sociality stimuli (e.g., stories about outdated pictures) as the control stimuli. However, Saxe and Wexler (2005) found that in one of these regions, i.e., the right TPJ, brain activation is sensitive not only to the social semantic richness of information but also to the congruence of it. Therefore, the function of the right TPJ should be related to integrating social- and/or mental-state-related information and making inferences with it, which is presumably a core function of ToM. The second function is the processing of relationality of concepts (Williams et al. 2017; Zhang and Pykkänen 2018). The relationality of a concept refers to the capacity of the concept to encode a relationship between entities. Representative examples with high relationality include verbs with complex argument structures (e.g., teach) and nouns denoting kinship (e.g., mother). The sociality and relationality of concepts are two related measures because a lot of relationships implied by word meanings are social relationships. It has been found that the left AG is involved in the processing of high-relationality words (Thompson et al. 2007, 2010; Williams et al. 2017; Zhang and Pykkänen 2018). However, it remains unclear whether the sociality and relationality effects in the left AG overlap with each other or whether one effect can explain the other. Further research is warranted to tease apart the activation of social concept representation from the functions of ToM and relationality.

The present study employed the contrast between semantically plausible and implausible phrases to explore the neural correlates of semantic plausibility judgment. Since the plausible conditions were easier than the implausible ones, one may suspect that the observed plausibility effect (plausible > implausible) is confounded by the effect of difficulty (easy > hard). Two recent studies found that the left AG is activated more by easy tasks than hard ones (Humphreys and Ralph 2017; Mattheiss et al. 2018). However, according to the reported peak coordinates, this difficulty-sensitive AG region is about 20 mm posterior and 10 mm inferior to the IPL region that showed the plausibility effect in the present study. More importantly, in our data analysis, the difficulty effect was largely eliminated by setting RT as a nuisance covariate. Therefore, the observed plausibility effect in the IPL is unlikely to reflect task difficulty.

It should be noted that although semantic plausibility is an important factor for the processing of conceptual combinations, its effect may not fully reveal the neural correlates of combinatorial conceptual processing. In addition, the relatively low temporal resolution of fMRI may restrict its ability to reveal the neural correlates of dynamic cognitive processes such as conceptual combination. For example, the present study did not find the semantic plausibility effect in the left ATL. However, some studies investigated the combinatorial processing of word meanings using other contrasts

(e.g., adjective-noun phrases versus isolated words) and techniques (e.g. MEG), and found the involvement of the left ATL (Bemis and Pykkänen 2011, 2013; Blanco-Elorrieta et al. 2018; Boylan et al. 2017; Forgács et al. 2012; Pykkänen et al. 2014; Zhang and Pykkänen 2015). There is also evidence that the left ATL is involved in the composition of sentence meaning (Pallier et al. 2011; Vandenberghe et al. 2002) and the same area is sensitive to social-emotional semantics (Mellem et al. 2016). Therefore, future studies are warranted to use other types of contrasts and techniques to further explore the overlap and dissociation between the neural correlates of social semantic processing and those of combinatorial conceptual processing.

In conclusion, we found that the brain regions sensitive to the social semantic richness of words and those sensitive to the semantic plausibility of phrases are largely dissociated from each other. The results of the present study, together with those of our recent study (Lin et al. 2018), indicate the existence of three adjacently distributed brain networks within the supramodal cortical semantic network, which are associated with social semantic processing, sensory–motor semantic processing, and semantic plausibility judgment, respectively. The dissociation between the three networks was also revealed by the RSFC data, indicating that the functional dissociation between the brain networks is associated with their underlying intrinsic connectivity structures.

Acknowledgements This work was supported by National Natural Science Foundation of China (Grant numbers: 31871105 and 31300842) and by CAS Key Laboratory of Behavioral Science. We thank Yu Wang for her help in the preparation of experiment and Xiaohong Yang for helpful discussions.

Funding This study was funded by National Natural Science Foundation of China (Grant numbers: 31871105 and 31300842) and by CAS Key Laboratory of Behavioral Science.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the Institutional Review Board of the Magnetic Resonance Imaging Research Center of the Institute of Psychology of the Chinese Academy of Sciences and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Informed consent Informed consent was obtained from all individual participants included in the study.

References

Ashburner J, Friston KJ (2005) Unified segmentation. *Neuroimage* 26(3):839–851

- Bemis DK, Pykkänen L (2011) Simple composition: a magnetoencephalography investigation into the comprehension of minimal linguistic phrases. *J Neurosci* 31(8):2801–2814
- Bemis DK, Pykkänen L (2013) Basic linguistic composition recruits the left anterior temporal lobe and left angular gyrus during both listening and reading. *Cereb Cortex* 23(8):1859–1873
- Binder JR, Conant LL, Humphries CJ, Fernandez L, Simons SB, Aguilar M, Desai RH (2016) Toward a brain-based componential semantic representation. *Cogn Neuropsychol* 33(3–4):130–174
- Binder JR, Desai RH (2011) The neurobiology of semantic memory. *Trends Cogn Sci* 15(11):527–536
- Binder JR, Desai RH, Graves WW, Conant LL (2009) Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb Cortex* 19(12):2767–2796
- Blanco-Elorrieta E, Ferreira VS, Del Prato P, Pykkänen L (2018) The priming of basic combinatory responses in MEG. *Cognition* 170:49–63
- Blank I, Balewski Z, Mahowald K, Fedorenko E (2016) Syntactic processing is distributed across the language system. *Neuroimage* 127:307–323
- Bonhage CE, Fiebach CJ, Bahlmann J, Mueller JL (2014) Brain signature of working memory for sentence structure: enriched encoding and facilitated maintenance. *J Cogn Neurosci* 26(8):1654–1671
- Boylan C, Trueswell JC, Thompson-Schill SL (2017) Relational vs. attributive interpretation of nominal compounds differentially engages angular gyrus and anterior temporal lobe. *Brain Lang* 169:8–21
- Chinese Linguistic Data Consortium (2003). [Chinese lexicon] (CLDC-LAC-2003-001) Beijing, China: Tsinghua University, State Key Laboratory of Intelligent Technology and Systems, and Chinese Academy of Sciences, Institute of Automation
- Contreras JM, Banaji MR, Mitchell JP (2012) Dissociable neural correlates of stereotypes and other forms of semantic knowledge. *Soc Cogn Affect Neurosci* 7(7):764–770
- Fernandino L, Binder JR, Desai RH, Pendl SL, Humphries CJ, Gross WL, Conant LL, Seidenberg MS (2016) Concept representation reflects multimodal abstraction: a framework for embodied semantics. *Cereb Cortex* 26(5):2018–2034
- Ferstl EC, Neumann J, Bogler C, von Cramon DY (2008) The extended language network: a meta-analysis of neuroimaging studies on text comprehension. *Hum Brain Mapp* 29(5):581–593
- Forgács B, Bohrn I, Baudewig J, Hofmann MJ, Pleh C, Jacobs AM (2012) Neural correlates of combinatorial semantic processing of literal and figurative noun noun compound words. *Neuroimage* 63(3):1432–1442
- Gallagher HL, Happe F, Brunswick N, Fletcher PC, Frith U, Frith CD (2000) Reading the mind in cartoons and stories: an fMRI study of ‘theory of mind’ in verbal and nonverbal tasks. *Neuropsychologia* 38(1):11–21
- Graves WW, Binder JR, Desai RH, Conant LL, Seidenberg MS (2010) Neural correlates of implicit and explicit combinatorial semantic processing. *Neuroimage* 53(2):638–646
- Hagoort P (2013) MUC (memory, unification, control) and beyond. *Front Psychol* 4:416
- Humphreys GF, Ralph MAL (2017) Mapping domain-selective and counterpointed domain-general higher cognitive functions in the lateral parietal cortex: evidence from fMRI comparisons of difficulty-varying semantic versus visuo-spatial tasks, and functional connectivity analyses. *Cereb Cortex* 27(8):4199–4212
- Humphries C, Binder JR, Medler DA, Liebenthal E (2006) Syntactic and semantic modulation of neural activity during auditory sentence comprehension. *J Cogn Neurosci* 18(4):665–679
- Huth AG, de Heer WA, Griffiths TL, Theunissen FE, Gallant JL (2016) Natural speech reveals the semantic maps that tile human cerebral cortex. *Nature* 532(7600):453–458

- Jung-Beeman M (2005) Bilateral brain processes for comprehending natural language. *Trends Cogn Sci* 9(11):512–518
- Lerner Y, Honey CJ, Silbert LJ, Hasson U (2011) Topographic mapping of a hierarchy of temporal receptive windows using a narrated story. *J Neurosci* 31(8):2906–2915
- Leslie AM (1994) Pretending and believing: issues in the theory of ToMM. *Cognition* 50(1–3):211–238
- Lin N, Bi YC, Zhao Y, Luo CM, Li XS (2015) The theory-of-mind network in support of action verb comprehension: evidence from an fMRI study. *Brain Lang* 141:1–10
- Lin N, Wang X, Xu Y, Hua H, Zhao Y, Li X (2018) Fine subdivisions of the semantic network supporting social and sensory–motor semantic processing. *Cereb Cortex* 28(8):2699–2710
- Lin N, Yu X, Zhao Y, Zhang M (2016) Functional anatomy of recognition of Chinese multi-character words: convergent evidence from effects of transposable nonwords, lexicality, and word frequency. *PLoS ONE* 11(2):e0149583
- Mahon BZ, Caramazza A (2009) Concepts and categories: a cognitive neuropsychological perspective. *Annu Rev Psychol* 60:27–51
- Martin A (2007) The representation of object concepts in the brain. *Annu Rev Psychol* 58:25–45
- Mattheiss SR, Levinson H, Graves WW (2018) Duality of function: activation for meaningless nonwords and semantic codes in the same brain areas. *Cereb Cortex* 28(7):2516–2524
- Mellem MS, Jasmin KM, Peng C, Martin A (2016) Sentence processing in anterior superior temporal cortex shows a social–emotional bias. *Neuropsychologia* 89:217–224
- Meyer ML, Spunt RP, Berkman ET, Taylor SE, Lieberman MD (2012) Evidence for social working memory from a parametric functional MRI study. *Proc Natl Acad Sci USA* 109(6):1883–1888
- Meyer ML, Taylor SE, Lieberman MD (2015) Social working memory and its distinctive link to social cognitive ability: an fMRI study. *Soc Cogn Affect Neurosci* 10(10):1338–1347
- Mitchell JP, Heatherton TF, Macrae CN (2002) Distinct neural systems subserving person and object knowledge. *Proc Natl Acad Sci USA* 99(23):15238–15243
- Pallier C, Devauchelle AD, Dehaene S (2011) Cortical representation of the constituent structure of sentences. *Proc Natl Acad Sci USA* 108(6):2522–2527
- Price AR, Bonner MF, Peelle JE, Grossman M (2015) Converging evidence for the neuroanatomic basis of combinatorial semantics in the angular gyrus. *J Neurosci* 35(7):3276–3284
- Pykkänen L, Bemis DK, Elorrieta EB (2014) Building phrases in language production: a MEG study of simple composition. *Cognition* 133(2):371–384
- Pykkänen L, Brennan J, Bemis DK (2011) Grounding the cognitive neuroscience of semantics in linguistic theory. *Lang Cogn Proc* 26(9):1317–1337
- Rice GE, Hoffman P, Binney RJ, Ralph MAL (2018) Concrete versus abstract forms of social concept: an fMRI comparison of knowledge about people versus social terms. *Philos Trans R Soc B* 373(1752):20170136
- Saxe R, Kanwisher N (2003) People thinking about thinking people: the role of the temporo-parietal junction in “theory of mind”. *Neuroimage* 19(4):1835–1842
- Saxe R, Wexler A (2005) Making sense of another mind: the role of the right temporo-parietal junction. *Neuropsychologia* 43(10):1391–1399
- Schurz M, Radua J, Aichhorn M, Richlan F, Perner J (2014) Fractionating theory of mind: a meta-analysis of functional brain imaging studies. *Neurosci Biobehav Rev* 42:9–34
- Shrout PE, Fleiss JL (1979) Intraclass correlations—uses in assessing rater reliability. *Psychol Bull* 86(2):420–428
- Silver NC, Dunlap WP (1987) Averaging correlation coefficients: should Fisher’s z transformation be used? *J Appl Psychol* 72(1):146–148
- Song XW, Dong ZY, Long XY, Li SF, Zuo XN, Zhu CZ, He Y, Yan CG, Zang YF (2011) REST: a toolkit for resting-state functional magnetic resonance imaging data processing. *PLoS ONE* 6(9):e25031
- Stowe LA, Broere CAJ, Paans AMJ, Wijers AA, Mulder G, Vaalburg W, Zwarts F (1998) Localizing components of a complex task: sentence processing and working memory. *NeuroReport* 9(13):2995–2999
- Tamir DI, Thornton MA, Contreras JM, Mitchell JP (2016) Neural evidence that three dimensions organize mental state representation: rationality, social impact, and valence. *Proc Natl Acad Sci USA* 113(1):194–199
- Thompson CK, Bonakdarpour B, Fix SC, Blumenfeld HK, Parrish TB, Gitelman DR, Mesulam MM (2007) Neural correlates of verb argument structure processing. *J Cogn Neurosci* 19(11):1753–1767
- Thompson CK, Bonakdarpour B, Fix SF (2010) Neural mechanisms of verb argument structure processing in agrammatic aphasic and healthy age-matched listeners. *J Cogn Neurosci* 22(9):1993–2011
- Tzourio-Mazoyer N, Landeau B, Papathanassiou D, Crivello F, Etard O, Delcroix N, Mazoyer B, Joliot M (2002) Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage* 15(1):273–289
- Vandenberghe R, Nobre AC, Price CJ (2002) The response of left temporal cortex to sentences. *J Cogn Neurosci* 14(4):550–560
- Wang X, Wang B, Bi Y (2019) Close yet independent: dissociation of social from valence and abstract semantic dimensions in the left anterior temporal lobe. *Hum Brain Mapp* 40(16):4759–4776
- Williams A, Reddigari S, Pykkänen L (2017) Early sensitivity of left perisylvian cortex to relationality in nouns and verbs. *Neuropsychologia* 100:131–143
- Xia MR, Wang JH, He Y (2013) BrainNet viewer: a network visualization tool for human brain connectomics. *PLoS ONE* 8(7):e68910
- Xu J, Kemeny S, Park G, Frattali C, Braun A (2005) Language in context: emergent features of word, sentence, and narrative comprehension. *Neuroimage* 25(3):1002–1015
- Xu YW, Lin QX, Han ZZ, He Y, Bi YC (2016) Intrinsic functional network architecture of human semantic processing: modules and hubs. *Neuroimage* 132:542–555
- Yarkoni T, Barch DM, Gray JR, Conturo TE, Braver TS (2009) BOLD correlates of trial-by-trial reaction time variability in gray and white matter: a multi-study fMRI analysis. *PLoS ONE* 4(1):e4257
- Yeo BTT, Krienen FM, Sepulcre J, Sabuncu MR, Lashkari D, Hollinshead M, Roffman JL, Smoller JW, Zoller L, Polimeni JR, Fischl B, Liu HS, Buckner RL (2011) The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *J Neurophysiol* 106(3):1125–1165
- Zahn R, Moll J, Krueger F, Huey ED, Garrido G, Grafman J (2007) Social concepts are represented in the superior anterior temporal cortex. *Proc Natl Acad Sci USA* 104(15):6430–6435
- Zhang LM, Pykkänen L (2015) The interplay of composition and concept specificity in the left anterior temporal lobe: an MEG study. *Neuroimage* 111:228–240
- Zhang LM, Pykkänen L (2018) Composing lexical versus functional adjectives: evidence for uniformity in the left temporal lobe. *Psychon Bull Rev* 25(6):2309–2322

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.